The masting species of New Zealand broadleaf-podocarp forests

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A thesis submitted in partial fulfilment of the requirements for the

Degree of Master of Science in Biology

School of Biological Sciences

University of Canterbury

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2018

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Abstract

Mast seeding is an evolved trait where individuals within a population synchronise their large interannual reproductive efforts, providing selective reproductive advantages. Synchronisation of large seed crops in masting species creates resource pulses for seed consuming species, with bottom up effects on local ecosystems. These bottom up effects may extend through multiple trophic levels, altering predator prey relationships. Large seed events of masting species in New Zealand forests have been associated with increased predator abundances and subsequent predation risk on native bird species. However, little is known about the masting characteristics of species in New Zealand's broadleaf-podocarp forests. To remedy this, I performed I analysis on 57 datasets, including 26 species, from eight broadleaf-podocarp forests in New Zealand. My thesis aimed to describe the masting characteristics of these species in a quantitative fashion. This involved quantifying the variability of these species, identifying relationships in synchrony (within and between species), and creating weather-based models to predict large seed events. I discovered that species in New Zealand's broadleaf podocarps form a continuous scale of masting intensity. Variability of species with fruit sizes > 10 mm were found to have low synchrony, which may be due to limited disperser species resulting in higher risk of disperser satiation. High levels of synchrony between geographically distant populations was found in hinau (*Elaeocarpus dentatus)*, kahikatea (*Dacrycarpus dacrydioides*), rimu (*Dacrydium cupressinum*) and supplejack (*Ripogonum scandensI*). Synchrony between populations of kahikatea occurred due to individuals synchronising with a floral cue involving summer temperatures. Large seed years in kahikatea occurred when warm summers in the year of floral initiation were preceded by cool summers in the previous year. Many species in broadleaf-podocarp forests were found to be highly

synchronous in their among year reproductive effort. This is likely due to a paucity of potential floral cues. No relationship was identified with variability of seed production and synchrony between species. This suggested that the highly variable species in broadleaf podocarp forests are not consistently synchronous. Lack of synchrony between the highly variable broadleaf-podocarp species likely reduces the size of resource pulses, creating more consistent among year resources for consuming species. Due to this, I suggest that pest management efforts should be more consistent than in forests with types with highly variable resource levels.

1 Introduction

1.1 Literature review

Mast seeding (masting) can be defined as synchronous, variable, seed production among years by a population of perennial plants (Janzen 1971, Silvertown 1980, Kelly 1994). This trait is observed globally, in both the northern (Sork et al. 1993, Koenig and Knops 2000, Suzuki et al. 2005) and southern (Kelly et al. 2000, Schauber et al. 2002) hemispheres. However, masting species are particularly common in New Zealand (Webb and Kelly 1993). The causes of masting can be examined at two levels: ultimate mechanisms and proximate mechanisms (Pearse et al. 2016). The ultimate mechanisms of masting are the selective reproductive advantages that have led to the evolution of the trait. The proximate mechanisms, however, are the environmental cues and physiological pathways that make this trait possible. Each of these mechanisms will be discussed separately.

Hypotheses surrounding the ultimate cause of masting rely on the principle of economies of scale (Janzen 1978, Norton and Kelly 1988, Kelly and Sork 2002). These hypotheses explain how large population-level reproductive efforts create greater reproductive efficiency for individuals, when compared to small reproductive efforts (Kelly and Sork 2002). Therefore, individuals that synchronise their large reproductive efforts will have greater fitness, hence masting will be selected for (Kelly and Sork 2002). Explanations of common hypotheses can be found in Table 1.1.

Table 1.1 Hypotheses of the ultimate cause of masting. Table adapted from Kelly (1994).

Hypothesis	Description
Wind pollination	The relationship between flowering effort and pollination success is non-linear, i.e. a larger flowering effort results in more efficient pollination success. Masting should therefore be selected for when pollination efficiency can be improved by a reproductive effort greater than the long-term mean. Contrastingly, masting should not be selected for when a population of plants can achieve maximum pollination efficiency every year (Kelly et al 2001).
Predator satiation	Variable and synchronous seed production lowers seed predator by saturating predators in high years and/or lowering predator abundance through starvation in low years, allowing for increased fitness in years of large reproductive effort.
Environmental prediction	Large reproductive efforts occur in anticipation of favourable environmental conditions for reproduction and establishment. As a result, seed and/or seedling survival is enhanced.
Animal pollination	Larger floral displays attract a greater number of animal pollinators, resulting in a higher total percentage of flowers pollinated, and therefore greater reproductive efficiency.
Animal dispersal	Larger fruit crops attract disproportionately more dispersers so a higher % of fruits are dispersed, or increase the distance of dispersal.

Conceptual modelling by Kelly et al. (2001) provided support for the wind pollination hypothesis in some species. Masting intensity is often calculated as a coefficient of variation, $\boldsymbol{CV = standard\ deviation/mean}$, being the standard deviation of the population level seed production among years divided by and mean population level seed production across years. Kelly et al. (2001) showed that reproductive efficiency in two *Nothofagus* species (*N. solandri* and *N. menziesii*), improved greatly with increasing flower crop size. Furthermore, for *N. solandri*, this relationship was found to strengthen with increasing altitude (which results in lowered mean seed output per individual), and with greater fragmentation (resulting in lowered mean flowering effort per unit area).

Predator satiation is the most commonly cited hypothesis to explain masting (Smith et al. 1990). This has been suggested to be the ultimate mechanism for masting in many *Chionochloa* species (Kelly et al. 2000, Rees et al. 2002). The selective advantages of masting

with regards to predator satiation have been well demonstrated in *C. pallens* (Kelly and Sullivan 1997). Kelly and Sullivan (1997) identified that the total percentage of florets destroyed by seed predators decreased with increasing variation among years. Kelly and Sullivan (1997) suggested this occurred, not due to the reproductive effort in a single year, but due to the change in reproductive effort between years. By having large intermittent reproductive episodes, *C. pallens* increases reproductive efficiency by decreasing the seed predator's ability to numerically respond to the large number of florets present in high reproductive effort years.

The remaining masting hypotheses have mixed support in the literature, or only apply to specific systems (Kelly 1994). Kelly (1994) found there was no evidence to generally support environmental prediction of favourable climates and that it was unlikely plant species could predict favourable climate conditions owing to the long time between flowering and seedling establishment, and the highly unpredictable nature of climates. However, masting has shown to be beneficial via environmental prediction specifically for some species in systems prone to fires (Peters et al. 2005), especially if species use the fires to predict favourable conditions (increased nutrient availability and reduced competition) (Kelly 1994). Masting may provide selective benefits in animal pollinated species, but alternatively it may reduce reproductive efficiency depending on the functional and numerical response of pollinator species (Kelly 1994). Large seed crops may increase the percentage of flowers pollinated, if generalist pollinators are attracted to large floral displays in great enough numbers. However, large seed crops may also decrease the total percentage of flowers pollinated if the pollinators become satiated. Similarly, masting may be selected for, or against, in animal dispersed species, depending on whether the numerical and functional response of dispersers is great enough to prevent satiation (Kelly 1994). It is likely that the ultimate mechanism of masting is species specific, and hypotheses may not be mutually exclusive.

Study of the proximate mechanisms of masting involves identifying the external cues allowing for the synchronisation of large reproductive efforts within populations. To allow individual variability of reproductive effort among years, yet synchrony between individuals, the external cues must be variable among years and consistent over geographical areas. Weather conditions (particularly temperature) have been proposed as the most likely external cue, being external, autocorrelated over large spatial scales, and influencing many metabolic processes such as photosynthesis and growth in plants (Schauber et al. 2002). For many species, larger than average seed years have been associated in some way with warm temperatures during floral initiation (summer). This has been observed, for example, in *Chionochloa* (Kelly et al. 2000, Kelly et al. 2013, Monks et al. 2016), *Fagus* (Suzuki et al. 2005), *Dacrydium* (Norton and Kelly 1988, Schauber et al. 2002), *Nothofagus*, *Elaeocarpus*, and *Phormium* (Kelly et al. 2013). While seedfall in some species has been associated with spring temperatures, and rainfall (Sork et al. 1993, Haase et al. 1995), it appears as though these relationships are much less common.

Research into predictive modelling of seedfall in masting species is a developing field. While early models showed that large seed years were strongly associated with warm summer temperatures in the year of floral induction for many species (the T1 model) (Kelly et al. 2000, Schauber et al. 2002, Masaki et al. 2008), recent studies have advanced on this model. Kelly et al. (2013) showed that variation seed production could be explained better (judged by AIC, RMSE, and confidence interval) by the difference in the mean summer temperatures for the two years preceding seedfall (the delta T model). This was a significant finding as not only did it improve our ability to predict future seed crops in many species, but it suggested that masting seeding may not be affected by climate change increasing long term mean temperatures (Kelly et al. 2013), as first thought (McKone et al. 1998). Until recently research had primarily focused on building empirical models, using long runs of seed data to detect correlations between

seedfall variation and weather variables (such as T1 and delta T). While empirical models may be able to explain patterns in a species interannual seed production, they have limited application for predicting future responses in changing climates as they do not attempt to understand the underlying biological mechanisms of mast seeding (Monks et al. 2016). However, a recent study by Monks et al. (2016) developed a mechanistic model of mast seeding in *Chionochloa*, involving what they termed a "resource-limited induction mechanism". By modelling the internal resource states of plants, in combination with external floral cues they created a model with greater than 8.7× the statistical support of previously developed *Chionochloa* models, including T1 and delta T. Furthermore, the resource-limited induction mechanism described by Monks et al. (2016), suggested that masting species would be sensitive to climate change.

Interest in masting lies not only in selective advantages, and proximate causes, but in the large ecological impacts masting species have on their communities. Masting species create variable resources for seed consuming species, with high seed years producing large resource pulses. Masting induced resource pulses can cause demographic responses from populations of seed consumers, resulting in strong bottom-up effects which permeate through the food web (Ostfeld and Keesing 2000, Kelly and Sork 2002, Kelly et al. 2008a). A North American study by McShea (2000) found that large seed crops from masting oak species (*Quercus* sp.), correlated with demographic responses from white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), and grey squirrels (*Sciurus carolinensi*). Furthermore, predation rates of artificial nests were found to be positively associated with large acorn crops in the previous autumn. McShea (2000) suggested this may be due to elevated abundances of carnivores that predate on the small mammals.

Similar patterns of bottom-up effects have been observed in New Zealand beech (*Nothofagus*) forests. Wilson et al. (1998) observed mouse (*Mus musculus*) abundances to

increase follow large seed years from a beech population. Wilson et al. (1998) noted that the bottom-up effect also extended another trophic level, with stoat (*Mustela erminea*) abundance also elevating with the increased availability of mouse prey. Furthermore, Wilson et al. (1998) implicated stoats as a primary driver of the decline of the kaka (*Nestor meridionalis*), a species endemic to New Zealand. The relationship between beech masts and increased predation pressures is, however, not unique to kaka. O'Donnell and Phillipson (1996) found that mouse and stoat densities, and predation rates on mohua (*Mohoua ochrocephala*), all increased following a large seed year from *Nothofagus* trees.

Mast events in New Zealand have not only been observed to have indirect effects on bird populations, through bottom-up and subsequent top-down effects, but also direct effects by affecting reproductive behaviour. In beech forests kaka have been found to only breed in years where beech seed production is high (Wilson et al. 1998). Similarly, on New Zealand offshore islands kakapo (*Strigops habroptilus*) have been observed to nest only in years where rimu (*Dacrydium cupressinum*) or pink pine (*Halocarpus biformis*) fruit is abundant (Powlesland and Lloyd 1994, Elliott et al. 2001, Harper et al. 2006).

While masting is clearly an import area of research in New Zealand, and globally, there has been a large over-representation in the literature of certain plant families. In a meta-analysis of masting behaviour in perennial plants, Kelly and Sork (2002) compiled an extensive list of masting datasets, a total of 571 datasets covering 168 different species. Of these datasets a total of 82.1% were of species belonging to five families: Pinaceae (48.9%), Fagaceae (16.6%), Betulaceae (8.1%), Fabaceae (5.1%), and Poaceae (3.5%). Only seven datasets (1.2%) were on species from the Podocarpaceae, and of these datasets, four were from the same monitoring site. Plant species from New Zealand’s broadleaf-podocarp forests are severely underrepresented in masting literature. There are, to my knowledge, only two published studies on the masting patterns of Podocarpaceae species. The first, Norton and Kelly (1988), focused

on a single species, rimu (*Dacrydium cupressinum*). While this study included many study years (33), seeds were only collected at one sampling location, and only from eight trays (each 0.86 m^2) which were not set to target individual trees. The second study, Beveridge (1973), included five podocarp species: rimu, miro (*Prumnopitys ferruginea*), matai (*Prumnopitys taxifolia*), totara (*Podocarpus totara*), and kahikatea (*Dacrycarpus dacrydioides*). However, sampling for this study only occurred at a single site (Pureora Forest), over seven years. Even in combination, these studies provide a narrow understanding of masting in podocarp species.

There is, therefore, a large gap in the current literature surrounding masting in broadleaf-podocarp forests. The Department of Conservation, with assistance from Landcare and the University of Canterbury, have established seed monitoring programs with the aim of filling this knowledge gap (as detailed below). My study is the first analysis on these datasets.

1.2 Thesis aims

My aim was to describe and interpret the masting characteristics of species in New Zealand's broadleaf-podocarp forests in a quantitative fashion. My specific aims were:

(1) To quantify the variation over years in seed crops (measured by the Coefficient of Variation, CV) for all the most abundant species in podocarp-broadleaf forest, including testing how consistent the CV was within a species across multiple sites.

(2) To quantify the level of synchrony in seed crops, both among sites for single species, and between different species at the same site.

(3) To test for correlations between seed crops and weather predictors which are potential synchronizing cues for mast seeding species.

1.3 Site descriptions

In a programme set up by the Department of Conservation in collaboration with Landcare Research and the University of Canterbury, seeds are being collected from eight different broadleaf-podocarp forests in New Zealand (Figure 1.1). Sampling was carried out in two scientific reserves (Blue Duck Reserve & Waipapa), two national parks (Okarito & Otamatuna), and four scenic reserves (Cascade Kauri Park, Pelorus Bridge, Paengaroa, and Trounson Kauri Park). The monitoring sites span a latitudinal range of 840 km, and an altitudinal range of 616 m (Table 1.2).

At monitoring sites, the area within which seed traps were located ranged in size, from 2-167 ha (Table 1.2). Climatically the sites also varied. Mean daily air temperatures ranged from 9.6°C at the coolest site (Blue Duck Reserve) to 14.9°C at the warmest site (Trounson Kauri Park) (Table 1.2). While absolute mean air temperatures vary among sites, all sites display similar seasonal patterns for air temperature (Figure 1.2). Yearly rainfall was variable among monitoring sites. Okarito received by far the most rain of the seedfall monitoring sites, with an annual mean of 3688 mm (Table 1.2). The remaining sites received considerably less rainfall, ranging between 1000-1650 mm per year (Table 1.2).

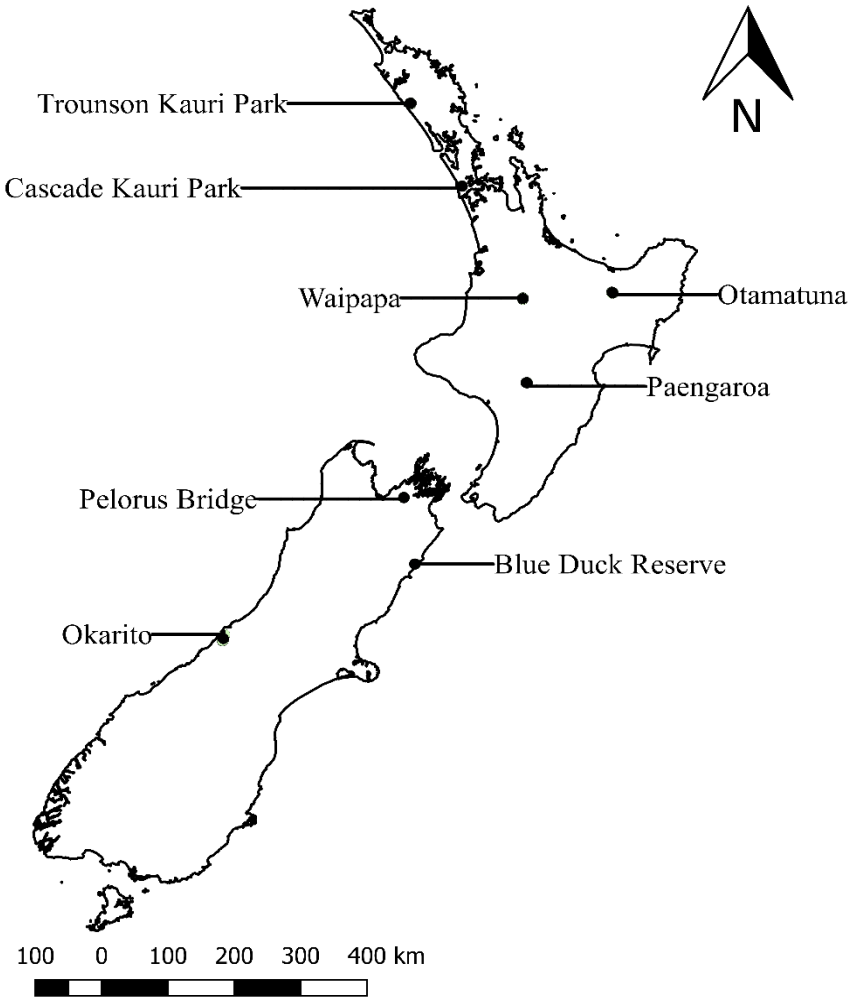

Figure 1.1 Locations of seedfall monitoring sites used in the study. Map generated using QGIS (Team 2012).

Table 1.2 Monitoring site attributes. Latitude, longitude and altitude are mean values of all seed traps used at the monitoring site. Mean daily temperature and mean annual rainfall are for the nearest virtual climate station from NIWA's network, for the years 2001-2017. Sampled area is the convex hull of all seed traps at each site (i.e. the area the seed traps were set up over).

Site	Latitude (S)	Longitude (E)	Altitude (m)	Mean temp (C)	Mean rainfall (mm)	Set up	Seed traps	Sampled area (ha)
Blue Duck	42 14.21	173 47.11	402	9.6	1095	Oct-03	60	6.6
Cascade	36 53.28	174 31.33	91	14.6	1639	June-13	74	48.5
Okarito	43 15.67	170 14.39	82	11.4	3688	May-12	30	2.1
Otamatuna	38 19.85	177 08.89	667	12.4	1990	May-08	65	159.4

Paengaroa	39 38.71	175 43.18	580	10.5	1083	May-09	63	68.2
Pelorus	41 17.90	173 34.57	51	13.0	1490	Feb-10	55	19.5
Trounson	35 43.49	173 38.54	255	14.9	1592	Oct-08	76	166.7
Waipapa	38 27.49	175 36.41	548	11.4	1568	May-08	73	80.4
Total							496	

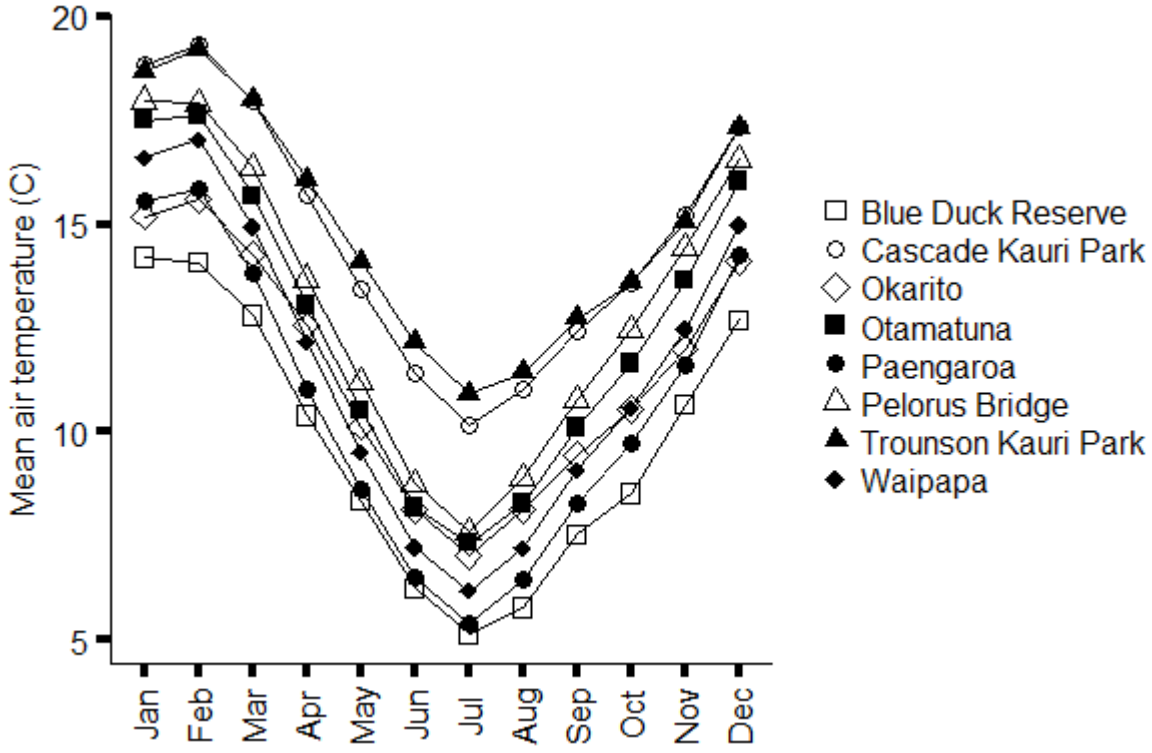

Figure 1.2 Monthly mean air temperatures for all monitoring sites used in the study. Data sourced from NIWA's virtual climate network by using closest virtual climate station, for the years 2001-2017.

1.4 Data collection

1.4.1 Seed collection

Permanent seed traps were installed by Neil Fitzgerald from Landcare Research (mean = 62 per site, min = 30, max = 74; Table 1.2). Seed traps were intentionally placed below individual trees of a target species (Figure 1.3), in order to have traps under at least 10 mature trees of each target podocarp species (selecting only females of dioecious species), and all

overhead tree species were recorded. Seed traps were a standard design with a capture area of 0.28 m^2 (Figure 1.4), except for some traps at Blue Duck Reserve pre-2011. At Blue Duck Reserve monitoring of a single species (*Beilschmiedia tawa*) was begun in October 2003 using 10 seed traps, each measuring 0.1 m^2 under different individual tawa trees. In 2006 two more traps (of the same size) were added under the same 10 tawa trees to expand the catch area to 0.3 m^2 for each tree. Finally, in 2011, 60 standard 0.28 m^2 traps were placed under 60 different individual trees of seven different species, including the 10 original tawa trees. At this time all the previous traps were removed. As a result, 60 traps targeted 60 individual trees at Blue Duck Reserve, from 2011 onwards. At all other sites seed traps were placed simultaneously and have not been altered. Seeds were collected from the seed traps multiple times per year, every year. However, for Paengaroa in 2013, there were no data as the collected samples were lost.

*Figure 1.3 A seed trap placed to catch from rimu (*Dacrydium cupressinum*, left) and kahikatea (*Dacrycarpus dacridioides*, right) trees at Blue Duck Reserve.*

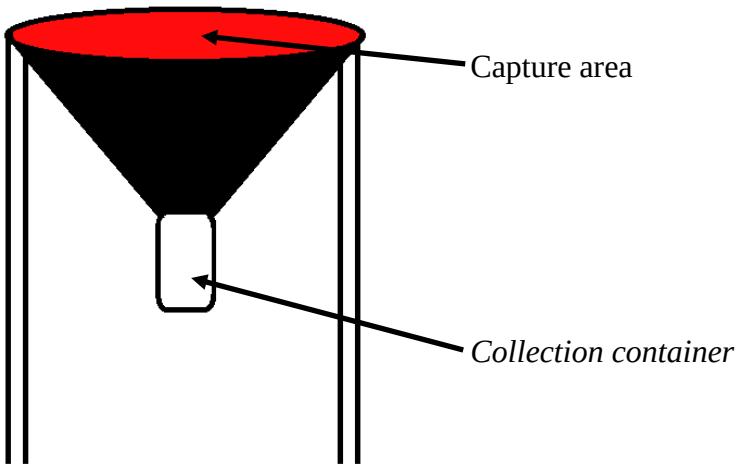

Figure 1.4 Diagram illustrating the capture area of a seed trap. Catch area (in red) = 0.28 m^2.

1.4.2 Seed identification and counting

Seeds were identified and counted by the University of Canterbury. Seeds were identified to the species level, for almost all seeds, based on seed morphology. Seeds that could not be identified to the species level were identified to the genus level when possible or were otherwise recorded as unknown. Seed samples from different traps were kept separate during the identification and counting process, allowing for the data to be analysed at the trap level. All seeds were separated by species, and then counted individually, except when a sample contained a large number of seeds from a single species. In that situation, 250 seeds were counted and weighed, then the remaining uncounted seeds were weighed. By using the weight of these counted and uncounted seeds, the total number of seeds of that species in the sample could be estimated.

1.4.3 Weather data

Weather data were obtained from the National Institute of Water and Atmospheric Research's (NIWA) virtual climate station network (VCSN). This network provides daily estimates of several climate variables including maximum-minimum air temperatures and rainfall, on a ~5 km grid over New Zealand. This is achieved using spatial interpolation of real data collected from climate stations around New Zealand. Weather variables used in this study were obtained from the closest virtual climate station. The closest virtual climate station for each monitoring site was on average 2.0 km away from centre of each monitoring site. Previous masting studies have often used the closest real climate station (Kelly et al. 2013, Monks et al. 2016), with some studies sourcing weather data from up to 50 km away (Norton and Kelly 1988). The recently developed VCSN provides estimated weather variables for locations often much closer to study sites than any real weather station.

1.5 Study species

Seeds of 26 species were counted in the seedfall datasets, from 16 different families, for which general information, including common and scientific names can be found in Table 1.3. Species will hereafter be referred to by their common names.

Table 1.3 Details for all study species. Fruit diameters included for all bird dispersed species that were identified to the species level. All fruit diameters sourced from Kelly et al. (2010), unless denoted otherwise.

Species	Common name	Family	Group	Dispersal mode	Fruit diameter (mm)
Agathis australis	Kauri	Araucariaceae	Gymnosperm	Wind	-
Beilschmiedia tarairi	Taraire	Lauraceae	Angiosperm	Bird	19.6
Beilschmiedia tawa	Tawa	Lauraceae	Angiosperm	Bird	15.5
Coprosma grandifolia	Coprosma grandifolia	Rubiaceae	Angiosperm	Bird	6.6
Corynocarpus laevigatus	Karaka	Corynocarpaceae	Angiosperm	Bird	17.5
Dacrycarpus dacrydioides	Kahikatea	Podocarpaceae	Gymnosperm	Bird	5.8[A]
Dacrydium cupressinum	Rimu	Podocarpaceae	Gymnosperm	Bird	2.0[B]
Dysoxylum spectabile	Kohekohe	Meliaceae	Angiosperm	Bird	9.0
Elaeocarpus dentatus	Hinau	Elaeocarpaceae	Angiosperm	Bird	9.2
Fuscospora cliffortioides	Mountain Beech	Nothofagaceae	Angiosperm	Wind	-
Fuscospora fusca	Red Beech	Nothofagaceae	Angiosperm	Wind	-
Hedycarya arborea	Pigeonwood	Monimiaceae	Angiosperm	Bird	9.7
Hoheria sp	Hoheria sp	Malvaceae	Angiosperm	Wind	-

Ixerba brexioides	Tawari	Strasburgeriaceae	Angiosperm	Bird	5.5[D]
Melicytus ramiflorus	Mahoe	Violaceae	Angiosperm	Bird	5.5[A]
Nestegis cunninghamii	Black Maire	Oleaceae	Angiosperm	Bird	9.6
Plagianthus regius	Lowland ribbonwood	Malvaceae	Angiosperm	Wind	-
Podocarpus acutifolius	Needle-leaved totara	Podocarpaceae	Gymnosperm	Bird	6.9[A]
Podocarpus cunninghamii	Mountain Totara	Podocarpaceae	Gymnosperm	Bird	5.0[A]
Podocarpus totara	Totara	Podocarpaceae	Gymnosperm	Bird	6.9[A]
Phyllocladus trichomanoides	Tanekaha	Podocarpaceae	Gymnosperm	Bird	4.0[C]
Pittosporum sp	Pittosporum sp	Pittosporaceae	Angiosperm	Bird	-
Prumnopitys ferruginea	Miro	Podocarpaceae	Gymnosperm	Bird	13.0
Prumnopitys taxifolia	Matai	Podocarpaceae	Gymnosperm	Bird	9.4
Ripogonum scandens	Supplejack	Ripogonaceae	Angiosperm	Bird	10.5
Vitex lucens	Puriri	Lamiaceae	Angiosperm	Bird	15.3

[A] *Janice Lord, University of Otago, pers. comm*

[B] *Rocío C. Jaña Prado, University of Canterbury, unpublished thesis*

[C] *University of Auckland, unpublished, retrieved from: http://www.nzplants.auckland.ac.nz*

[D] *Webb and Simpson (2001)*

2 Variability

2.1 Introduction:

While there has been much research on "masting" or "masting species", these terms have not yet been quantitatively defined. The literature suggests attempts to categorise species into groups of "masting" and "non-masting" species are ambiguous, subjective, and ultimately, ecologically irrelevant (Kelly 1994, Herrera et al. 1998). Instead, studies have shown the masting trait forms a continuous scale of intensity, from species of highly variable interannual seed production, to those with consistent levels of seed production between years (Kelly 1994, Herrera et al. 1998). The question therefore becomes, not whether a species is "masting" in a dichotomous sense, but where does a species fit on the masting scale quantitatively?

Masting intensity for a species is often quantified as the coefficient of variation. The coefficient of variation is calculated by dividing the standard deviation of the annual total seed production for a species at a site by the mean annual seed production of this species at this site ($CV=\sigma/\mu$). While many species' CVs have been calculated, positioning them on the masting scale, the majority of published masting datasets have been for species belonging to the families of Pinaceae, Fagaceae, Betulaceae, Fabaceae, and Poaceae (Kelly and Sork 2002). Little attention has been given to the ecologically significant species that make up New Zealand's broadleaf-podocarp forests. Kelly and Sork (2002) compiled a list of published masting datasets for a meta-analysis on the masting trait. Only seven of the 571 (1.2%) datasets included were for species from the Podocarpaceae family, with many species that are found in New Zealand broadleaf-podocarp forests having no published datasets. Quantifying the variability of the species that make up New Zealand's broadleaf-podocarp forests will increase our ability to make informed conservation decisions to protect New Zealand's native and endemic bird species that reside in them. By understanding the variability of our frugivorous bird species' food resources, we may

aid population recovery of endangered and threatened species through supplementary feeding. Supplementary feeding is a conservation strategy currently employed to aid kakapo (*Strigops habroptilus*) population recovery, and has been found to be highly successful in increasing breeding frequency (Elliott et al. 2001). By identifying which tree species are highly variable in their seed production, and which threatened birds rely on them, we may be able to identify which bird species would benefit the most from supplementary feeding programs.

The masting trait is also an area of interest in an evolutionary context, with previous studies aiming at identifying the ultimate evolutionary mechanisms that determine how variable a species is in its interannual seed production (Kelly 1994, Kelly and Sork 2002, Koenig and Knops 2005). Evolutionary mechanisms that are suggested to select for increased variability of interannual seed production rely on the concept of economies of scale (EOS). This states that larger than average reproductive efforts, synchronised between individuals within the population, increase reproductive efficiency (Norton and Kelly 1988). Potential EOS reproductive benefits include: increased pollination rates for wind pollinated species, satiation of seed predators, environmental prediction of favourable reproductive and establishing conditions, and many more (Kelly 1994). The reproductive benefits obtained through variable seed production, vary between species, and may be dependent on the species life history traits. One such life history trait that has been found to be associated with seed production variability is dispersal mode. A study by Herrera et al. (1998) found that species that rely on mutualistic frugivores for dispersal were on average less variable than species that are dispersed via inanimate means. It has been suggested that species that are dispersed by mutualistic frugivores are limited in their variability of seed production, as larger than normal seed years would satiate dispersers, leading to dispersal failure and a diseconomy of scale (Kelly 1994, Herrera et al. 1998). However, risk of dispersal failure may not be equal between frugivore dispersed species. Species with a low number of specialist disperses are likely at a higher risk of dispersal failure with increasing variability of seed

production. This is due to specialist dispersers lacking alternative food sources in low seed years, resulting in reduced abundances and subsequently having a greater chance of becoming satiated in high seed years. Conversely, species with many generalist dispersers would be at a lowered risk of dispersal failure with increasing variability, as dispersers can consume alternative food sources during low seed years, sustaining their population. As such, I hypothesise that species in New Zealand's broadleaf-podocarp forests that produce small fruits, able to be consumed by many bird species, should be more variable in their seed production than those with larger fruits which are dispersed by fewer, larger birds.

Differences in variability of seed production has been observed not only between species, but within species among populations (Webb and Kelly 1993, Kelly et al. 2000, Koenig and Knops 2000, Sullivan and Kelly 2000, Schauber et al. 2002, Kelly et al. 2013). As to why a species may have differing levels of variability between sites, it may relate to the productivity of the sites in question. Kelly and Sork (2002) hypothesised that plants in less productive habitats should display greater variability in their interannual seed production, as acquisition of resources would occur at slower rates at these sites, increasing the time between high seed years. This hypothesis has been supported through the observation of species with increasing levels of variability across productivity gradients. *Nothofagus solandri*, *Picea abies*, and species of *Chionochloa*, have all been shown to have greater variabilities of seed production at higher altitudes (Allen and Platt 1990, Webb and Kelly 1993, Mencuccini et al. 1995, Sullivan and Kelly 2000, Kelly et al. 2001). Latitude and soil fertility have also been suggested as habitat productivity variables that may affect a populations variability of seed production (Janzen 1974, Kelly and Sork 2002). It is, however, not known if species that make up New Zealand's broadleaf-podocarp forests also display this pattern. Furthermore, much of the previous research has focused on single species and therefore it is also unknown if this relationship can be generalised across plant communities or if it is species specific.

In this chapter I aim to quantify the variability of species in New Zealand broadleaf-podocarp forests and attempt to explain patterns of variability, within, and between species. In doing so, I will answer the following questions:

1. How variable are species in New Zealand broadleaf-podocarp forests, at the population level, compared to elsewhere?
2. Do species with small fruits display greater population level variability of seed production?
3. Are populations in less productive environments more variable in their interannual seed production?

2.2 Methods

2.2.1 Data checking

The structure of the data was unbalanced among species due to the sampling design of the study (described in Chapter 1:1.4). Datasets for each species were, therefore, not of equal quality. While data quality is difficult to quantify, and to some extent subjective, two primary attributes are important in a masting dataset. These attributes are sampling intensity (the number of trees sampled at a site) and the number of years of data. Masting is a population level phenomenon, involving the variability of individuals and the synchrony between these individuals (Kelly and Sork 2002, Koenig et al. 2003, Koenig et al. 2015). Therefore, the number of individuals sampled must be adequate to fairly represent these characteristics. For this purpose, I set the minimum number of trees sampled for dataset inclusion to five.

As large seed years in podocarp species have been observed to be periodic (Beveridge 1973), a dataset should be long enough to ensure a large seed event is captured. Capturing a large seed event is important as it can have a large effect on the calculated CV value. In a

metanalysis of masting Herrera et al. (1998) set the lower limit of years for dataset inclusion to 4, while Kelly and Sork (2002) only used datasets with >5 years of data. The minimum dataset length for inclusion in the current study was three years. The decision to include short datasets was made to increase the geographic range of the study, while also increasing the number of replicates for statistical analysis. This data selection process resulted in a total of 57 datasets, covering 26 different species (Table 2.1). The mean number of sampling years per species, all datasets included, was 12.9.

The final procedure used to ensure the data was of the highest quality possible was to remove "bycatch". Seeds from species not recorded as overhead of the trap were often found in the seed samples (i.e. bycatch). These were removed from the data, leaving only seed counts from the targeted trees recorded as overhead. Removal of bycatch was essential to allow for the conversion of seed counts to seeds m^{-2} under parent canopies. Seed counts had to be converted to seeds m^{-2} as the number of seed traps at Blue Duck Reserve was not consistent through the entirety of the sampling period. This conversion standardised the counts.

Table 2.1 The number of individual trees sampled of each species, at each site. Dashes indicate fewer than five individuals were sampled. Species are ordered by the total number of years of data. Scientific names can be found in Chapter 1: Table 1.3

Species	Blue Duck Reserve	Cascade Kauri Park	Okarito	Otamatuna	Paengaroa	Pelorus Bridge	Trounson Kauri Park	Waipapa	Total number of sites (datasets)	Total years
Kahikatea	10	10	11	-	11	10	6	12	7	40
Tawa	15[A]	12	-	23	-	10	5	54	6	39
Rimu	11	11	-	10	-	5	-	14	5	31
Miro	-	10	10	10	-	10	-	11	5	30
Hinau	11	-	-	10	-	10	-	11	4	28
Matai	15	-	-	-	7	10	-	13	4	25
Supplejack	13	11	-	16	-	-	-	18	4	24
Totara	11	-	-	-	-	-	-	10	2	13
Kauri	-	18	-	-	-	-	9	-	2	11
Mahoe	23	19	-	-	-	-	-	-	2	8
Kohekohe	-	-	-	-	-	-	7	-	1	8
Mountain Totara	-	-	-	11	-	-	-	-	1	8
Red Beech	-	-	-	10	-	-	-	-	1	8
Taraire	-	-	-	-	-	-	17	-	1	8
Tawari	-	-	-	14	-	-	-	-	1	8
Black Maire	-	-	-	-	10	-	-	-	1	5
Coprosma grandifolia	-	-	-	-	15	-	-	-	1	5
Hoheria sp	-	-	-	-	11	-	-	-	1	5
Lowland ribbonwood	-	-	-	-	5	-	-	-	1	5
Mountain Beech	11	-	-	-	-	-	-	-	1	5

Pittosporum sp	-	-	-	-	15	-	-	-	1	5
Needle-leaved totara	-	-	9	-	-	-	-	-	1	4
Karaka	-	10	-	-	-	-	-	-	1	3
Pigeonwood	-	7	-	-	-	-	-	-	1	3
Puriri	-	10	-	-	-	-	-	-	1	3
Tanekaha	-	11	-	-	-	-	-	-	1	3
First data year	2011	2014	2013	2009	2010	2010	2009	2009		
Total data years	5	3	4	8	5	7	8	8		

[A] *Ten individual tawa trees sampled from 2003-11 increased to 15 individual tawa trees from 2011-15. All other species at Blue Duck Reserve were targeted from 2011-15.*

2.2.2 Quantifying variability

Variability of seed production was quantified for each dataset by calculating the population level coefficient of variation (CV=σ/μ). CV is a commonly used unit in comparative studies of seedfall variability as it allows for comparisons of species that produce vastly different quantities of seed by creating a unit that is independent from the mean (Webb and Kelly 1993, Kelly et al. 2000, Kelly et al. 2001, Burns 2012).

CV values were calculated using the yearly total captured seed from targeted traps for all datasets apart from tawa at Blue Duck Reserve. The seed trapping effort (number of traps) was not consistent through the tawa time series at Blue Duck Reserve (see Chapter 1: 1.5.1 Seed collection) As such, seedfall was standardised to units of captured seeds per m^{-2} of trap area.

2.2.3 Variability and fruit size

Of the 26 species in this study 21 have adaptions for animal dispersal (Chapter 1: Table 1.3). Fruit diameter was used as the measure of fruit size as it is the diameter of the fruit, in combination with the birds gape size, that restricts consumption (Wheelwright 1985, Mazer and Wheelwright 1993). A linear regression was run to test for a relationship between a species fruit size and the variability of fruit production (CV) for that species. For species that had datasets from more than one site**,** a mean CV was used.

2.2.4 Variability and site productivity

Proxies of site productivity were selected from geographic and weather variables. Altitude and latitude were selected as they provide temperature gradients, which are known to be associated with productivity in plants (Körner 2007, Wang et al. 2007). The altitude and latitude for each population was taken as the mean altitude and latitude for all traps at each site. Mean air temperature and mean annual rainfall were selected as both are related to nutrient mineralisation (Sierra 1997, Smaill et al. 2011) and photosynthetic efficiency (Olesen and

Bindi 2002). They were selected over alternative measures, such as soil moisture and soil temperature, as they are less dependent on aspect, and therefore more general for the area. Mean air temperature was calculated as the mean of the daily maximum and minimum temperatures. All weather data was extracted from NIWA's virtual climate station network (described in Chapter 1:1.4.3).

The effects of productivity on variability of seed production were tested by fitting generalised linear mixed models (GLMM). The GLMM used species as a random term, as this allows for the data structure, where sites serve as replicates within species.

2.3 Results

2.3.1 Variability

The 26 species exhibited a wide range of CVs (Figure 2.1). The species' mean CV values were normally distributed (Shapiro-Wilk: $W = 0.98$, $p = 0.46$), with a mean of 1.06 and a standard deviation of 0.39. The most variable species was from the genus *Hoheria* (unidentified species), with a CV of 1.97 (n = 5 yr, one site), and the least variable species was needle-leaved totara, with a CV of 0.29 (n = 4 yr, one site) (Figure 2.1). As both these species have only short datasets they should be interpreted with caution. While some species with datasets from multiple sites were relatively consistent in their variability across sites (Table 2.2), such as miro and tawa, others, including kauri, were much less consistent.

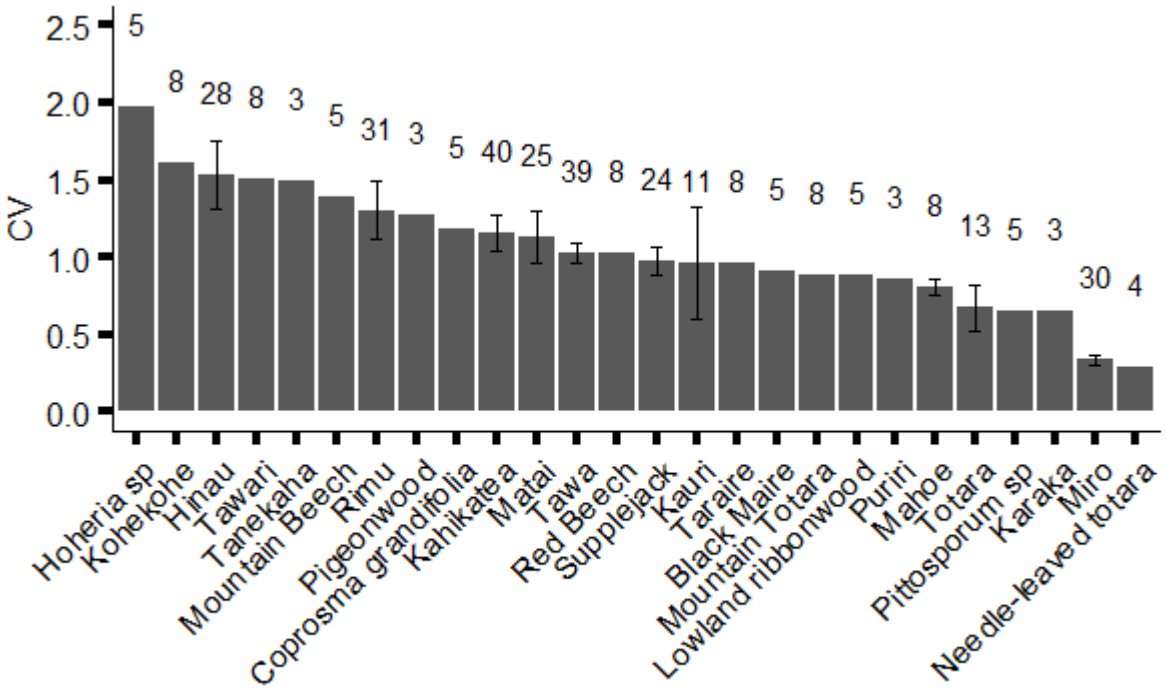

Figure 2.1 Variability of seed production (CV) for species with datasets meeting the criteria described in 2.2.1: Data checking. Species multiple datasets are displayed as a mean CV, with the standard error of this calculation included. Species lacking error bars only have a single dataset. Total number of years, including all datasets listed above columns.

Table 2.2 CV values for all species meeting the criteria described in section 2.3.1, including the mean CV value across all sites (national average), and the standard error of this calculation. Ordered by highest, to lowest national average CV.

Species name	Blue Duck Reserve	Cascade Kauri Park	Okarito	Otamatuna	Paengaroa	Pelorus Bridge	Trounson Kauri Park	Waipapa	Total yrs	Mean CV	Standard error
Hoheria sp	-	-	-	-	1.98	-	-	-	5	1.98	-
Kohekohe	-	-	-	-	-	-	1.61	-	8	1.61	-
Hinau	1.92	-	-	0.90	-	1.71	-	1.57	28	1.53	0.22
Tawari	-	-	-	1.50	-	-	-	-	8	1.50	-
Tanekaha	-	1.49	-	-	-	-	-	-	3	1.49	-
Mountain Beech	1.39	-	-	-	-	-	-	-	5	1.39	-
Rimu	0.97	1.19	-	1.10	-	2.01	-	1.25	31	1.30	0.18
Pigeonwood	-	1.27	-	-	-	-	-	-	3	1.27	-
Coprosma grandifolia	-	-	-	-	1.19	-	-	-	5	1.19	-
Kahikatea	0.92	1.25	1.70	-	0.82	1.18	0.88	1.32	40	1.15	0.12
Matai	1.45	-	-	-	0.66	1.10	-	1.32	25	1.13	0.17
Red Beech	-	-	-	1.03	-	-	-	-	39	1.03	-
Tawa	1.00	0.78	-	1.00	-	1.01	1.19	1.18	8	1.03	0.06
Supplejack	0.73	1.17	-	1.00	-	-	-	1.00	24	0.97	0.09
Kauri	-	1.32	-	-	-	-	0.60	-	11	0.96	0.36
Taraire	-	-	-	-	-	-	0.96	-	8	0.96	-
Black Maire	-	-	-	-	0.91	-	-	-	5	0.91	-
Mountain Totara	-	-	-	0.89	-	-	-	-	8	0.89	-
Lowland ribbonwood	-	-	-	-	0.88	-	-	-	5	0.88	-
Puriri	-	0.86	-	-	-	-	-	-	3	0.86	-
Mahoe	0.75	0.86	-	-	-	-	-	-	8	0.81	0.06
Totara	0.52	-	-	-	-	-	-	0.82	13	0.67	0.15
Karaka	-	0.65	-	-	-	-	-	-	3	0.65	-
Pittosporum sp	-	-	-	-	0.65	-	-	-	5	0.65	-

Miro	-	0.25	0.33	0.37	-	0.44	-	0.30	30	0.34	0.03
Needle-leaved totara	-	-	0.29	-	-	-	-	-	4	0.29	-

2.3.2 Variability and fruit size

Fruit sizes were obtained for all bird dispersed species in the study **(**Chapter 1: Table 1.3**)**. *Pittosporum* sp was not included as it was only identified down to the species level, meaning it was not possible to obtain a fruit size. The study species provided a large range of fruit sizes, with the largest being produced by taraire (19.6 mm diameter) and the smallest being produced by rimu (2.0 mm diameter) (Chapter 1:Table 1.3). The linear regression was not significant ($F = 2.06$, $n = 20$, $P = 0.168$, $r^2 = 0.10$) (Figure 2.2), although the trend was in the predicted direction.

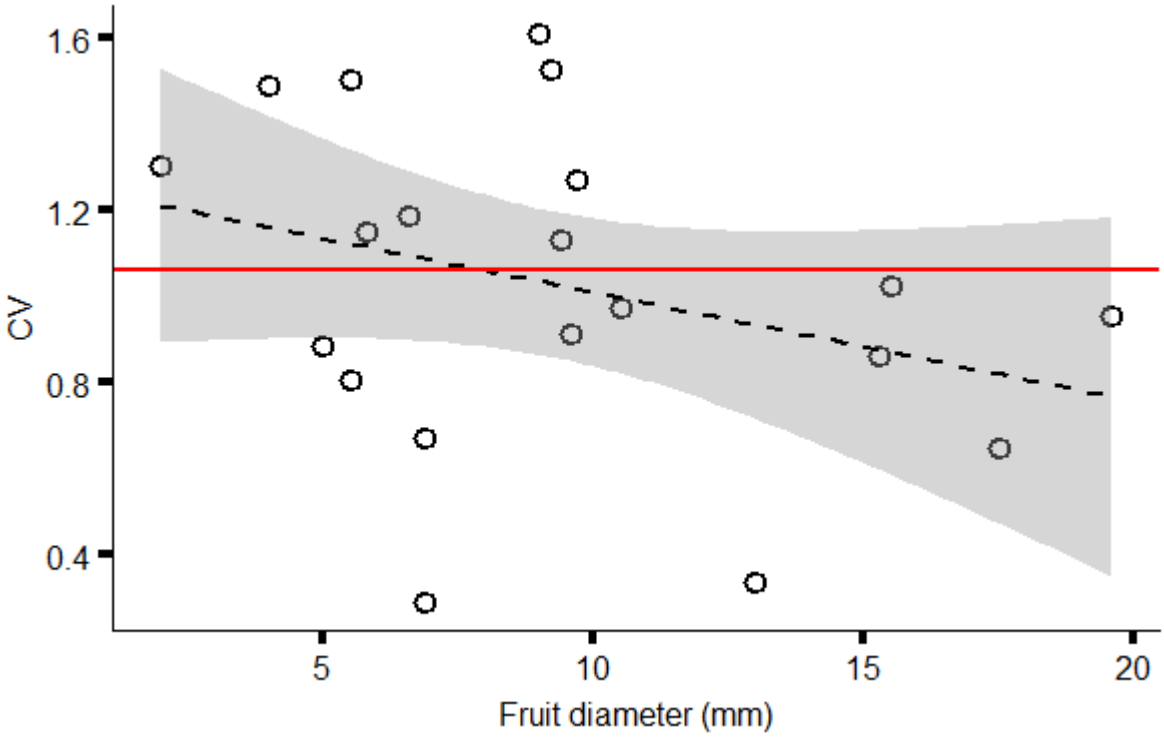

Figure 2.2 The relationship between fruit between fruit size and variability of fruit production (CV). Nonsignificant linear model indicated by the dashed line, standard error included. Mean CV (1.06) indicated by the solid red line.

While the linear model was insignificant, no species with fruits greater than 10 mm in diameter had CVs greater than the mean CV of all species (1.06) (Figure 2.2). A post hoc Fisher

exact test confirmed that species with fruits larger than 10 mm were significantly more often below the mean CV value than expected ($p = 0.02$).

2.3.3 Variability and site productivity

Of the 26 species in this study, 10 had datasets from multiple sites (Table 2.1). The CV values varied between sites, within species (Table 2.2). While species were not equally variable across sites, these differences in variability were not related to site productivity. All models created using logical combinations and interactions of site productivity measures provided a poor fit against variability of seed production (CV), when controlling for species (Table 2.3). Model 1, containing the single altitude variable, was the best fit (as judged by AIC, Table 2.3), however, the relationship was not significant (Figure 2.3).

Table 2.3 Results of GLMMs with species as a random term, ranked by AIC score.

Model	Variables	DF	F Value	P	AIC	R^2 Marginal	R^2 Conditional
Model 1	Altitude	1, 41.82	1.85	0.18	63.29	0.02	0.56
Model 2	Latitude	1, 43.09	0.26	0.61	64.69	0.00	0.51
Model 3	Mean rain per day	1, 46.04	0.04	0.85	65.78	0.00	0.51
Model 4	Mean air temperature	1, 46.27	0.13	0.72	66.22	0.00	0.50
Model 5	Altitude	1, 41.65	1.68	0.20	69.52	0.02	0.56
	Latitude	1, 41.25	0.18	0.67			
Model 6	Mean air temperature	1, 43.74	0.11	0.75	73.38	0.00	0.50
	Mean rain per day	1 44.80	0.01	0.92			
Model 7	Altitude	1, 39.19	2.07	0.16	74.30	0.03	0.59
	Latitude	1, 36.39	0.04	0.83			
	Altitude:Latitude	1, 36.70	0.83	0.37			
Model 8	Mean air temperature	1, 31.61	1.69	0.20	77.05	0.02	0.53
	Mean rain per day	1, 32.12	1.65	0.21			
	Mean air temperature: Mean rain per day	1, 32.05	1.64	0.21			

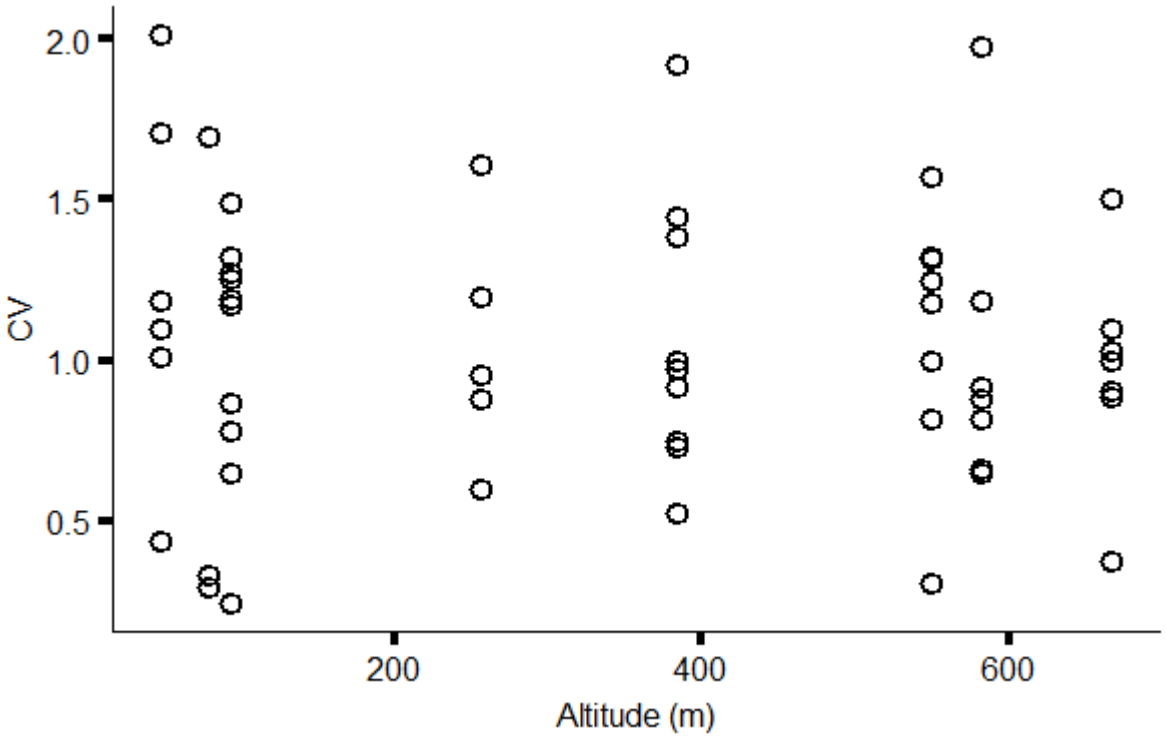

Figure 2.3 The relationship between altitude and variability of fruit production (CV). Note that this scatterplot is incapable of visualising the random term (species) used in the GLLM model from Table 2.3.

2.4 Discussion

2.4.1 Variability of seed production

It has been previously suggested that while masting may be an adaptive trait possessed by some species, the trait forms a continuous scale of intensity, and as such, separating species into categories of "masting" and "non-masting" is an ambiguous and subjective distinction (Kelly 1994, Herrera et al. 1998). My results support this with CVs for species in New Zealand podocarp forests being normally distributed. As CVs were not bimodally distributed there were no clear "masting" and "non-masting" species in the current study. This study has, however, identified many species that are highly variable at a population level.

Kelly et al. (2001) hypothesised that, in the absence of selective benefits or disadvantages of masting, species would have CV values in the range of 0.85-1.35. In the

current study I identified six species (hoheria sp, kohekohe, hinau, tawari, tanekaha, and mountain beech) with CVs exceeding 1.35. Mountain beech is a well-documented masting species, Webb and Kelly (1993) reported a similar CV value. A conceptual model by Kelly et al. (2001) identified mountain beech to receive large pollination benefits with greater population level seedfall, and this is likely the selective benefit for this species. As little is known about the other high CV species in my study it is difficult to determine the selective advantages, however, this presents an area for future research. While most of the species with CV values greater than 1.35 have small, and often only one, dataset, hinau was well sampled in the current study. With four datasets, and a total of 28 years of data, it seems unlikely that hinau's high CV has anything other than a biological basis. Therefore, hinau poses as an excellent candidate for future mast seeding research.

I have also identified six species (mahoe, totara, karaka, pittosporum sp, miro, and needle-leaved totara) with CVs lower than Kelly et al. (2001) expected to occur without selection. Again, little is known about these species as this is the first available dataset on these species, with the exception of miro. Beveridge (1973) reported on seven years of miro seedfall data. While no CV value was reported for miro, Beveridge (1973) monitoring little variation in miro seedfall, consistent with my findings.

2.4.2 Variability and fruit size

Species with high CVs may have evolved due to masting providing selective advantages (Kelly and Sork 2002). Selection for, or against, high variability of seed production may depend on the life history traits of the species in question. Dispersal mode has previously been shown to be one life history trait that effects the degree of masting (Herrera et al. 1998). Herrera et al. (1998) found that species that that rely on mutualistic frugivores for dispersal had lower CVs and suggested this to be due to selection against satiating dispersers during large

reproductive efforts. However, 21 of 26 species in the current study are bird dispersed (Chapter 1: Table 1.3), and yet a range of mean CVs were observed.

The level of mean CVs was not explained by variation in fruit size. While I hypothesised that species with smaller fruits would be more variable, owing to a greater abundance of generalist dispersers making disperser satiation unlikely, this was not supported by the result. The larger fruited study species do, however, seem to conform to this relationship. None of the species with fruits greater than 10 mm in diameter (these being: taraire, karaka, tawa, puriri, miro, and supplejack) exceeded the mean CV value of 1.06. When species were separated into categories of fruits ≥10 mm and fruits < 10 mm, it was discovered that having fruit sizes < 10 mm significantly increase the probability of the species having a CV less than the mean value of 1.06. I suggest that while the number of potential dispersers, and subsequently the risk of disperser satiation, may be a factor influencing the upper limit of variability for some species, this limit is not always realised, owing to a combination of alternative and apposing selective forces.

Herrera et al. (1998) suggested lowered variability of interannual seed production should be selected for in species dispersed by mutualistic frugivores, however, others argue variability may still offer economies of scale for this dispersal mode. Large synchronised fruiting efforts have been suggested to attract generalist dispersers due to increased foraging efficiency (Bawa 1980, Kelly 1994). This hypothesis may explain why high levels of variability are observed in the current study, despite study most study species being bird dispersed. Additionally, it could also explain why higher variability is more often observed in the smaller fruited species (i.e. those with generalist dispersers). However, as previously mentioned, this relationship is not consistent across all small fruited species. This is likely due to opposing selective forces relating to economies of scale. Highly variable seed production may be selected against due to factors such as increased density-dependent mortality (Hett 1971), as well as the

potential for missed opportunities for colonisation (Waller 1979). Therefore, in the absence of selective advantages for variable seed production, or in the presence of selective disadvantages for variable seed production, I would be expected that a small fruited species would be no more variable than a large fruited species.

2.4.3 Variability and site productivity

The hypothesis put forward by Kelly and Sork (2002) that "Plants in less productive habitats should show more pronounced masting.", was not supported by this study. None of the examined proxies of productivity had significant effects on within species variability of CVs. While altitude was the best predictor of CV, the model had a poor fit, and was not statistically significant (Table 2.3, Figure 2.3). This opposes Kelly and Sork (2002), who explicitly stated altitude to be a factor associated with productivity and masting intensity. Kelly and Sork (2002) cited five previously published studies which support their hypothesis. However, of these studies, four focus on a single species (Allen and Platt 1990, Mencuccini et al. 1995, Sullivan and Kelly 2000, Kelly et al. 2001), of which no podocarp species are included. The final study, Webb and Kelly (1993), involved multiple species (including some podocarps), however, in their study a single linear regression was used to analyse the effect of altitude on variability of seed production (all species included in the single model). Linear regression does not control for species (unlike the GLMM used in the current study), therefore the observed effect of altitude on masting intensity includes both within species variation, and between species variation. As such, the study by Webb and Kelly (1993) is statistically flawed and does not provide evidence that all species are more variable in less productive habitats. My results show that the hypothesis that plants in low productivity environments will display greater variability of seed production cannot be generalised to all species, instead I suggest this is a species-specific relationship.

Failure to detect this relationship in the current study is likely due to the inclusion of non-masting species. The studies that have shown support for the productivity-variability hypothesis in single species, have used species well known for their variable seed production: *Nothofagus solandri* (Allen and Platt 1990, Kelly et al. 2001), *Picea abies* (Mencuccini et al. 1995), and *Chionochloa* sp (Sullivan and Kelly 2000). These species likely achieve greater reproductive efficiency with intermittent large seed crops, through one of the hypothesises relating to economies of scale (Kelly 1994). Therefore, these species would benefit from accumulating resources through years, allowing for intermittent larger than average reproductive efforts. If these a species accumulate resources in this fashion, then the hypothesis of Kelly and Sork (2002), should hold true as these resources will take longer to accumulate in low productivity environments. However, the current study is not limited to highly variable species, with the study species displaying a wide range CVs (Figure 2.1). The study species with low CV values likely gain no reproductive benefit from synchronised, larger than average reproductive efforts, and subsequently are unlikely to accumulate resources through years for reproduction. Therefore, if resources are not accumulated through years, then the productivity of the environment would have no effect on the variability of the species seed production. As I have identified species that some species in broadleaf-podocarp forests have high CV values, it is likely that these species do accumulate resources through years and should subsequently display the productivity-variability relationship. However, due to the low number of datasets for many of the study species, it is not possible to investigate this relationship at an individual species level.

3 Synchrony

3.1 Introduction

Synchronisation of population dynamics over spatial scales is a reoccurring theme in nature. It is a phenomenon that has been observed in both the animalia (Ranta et al. 1997, Liebhold et al. 2004a) and plantae (Schauber et al. 2002, Yasaka et al. 2003, Koenig and Knops 2013) kingdoms. This field of research can be broken down into two categories: intraspecific synchrony and interspecific synchrony.

Intraspecific synchrony describes the synchrony of population dynamics within a species, between spatially distinct populations. For studies on masting plant species the population dynamic of interest is the yearly reproductive effort. Synchronisation of yearly reproductive efforts in masting species is suggested to occur via external floral initiation cues (Kelly 1994, Schauber et al. 2002). The presence of floral initiation cues within a species may therefore be inferred by high levels of synchrony between spatially distinct populations. For many masting species the floral initiation cue responsible for large seed years often relates in some way to air temperature during floral initiation (Norton and Kelly 1988, Kelly et al. 2013, Monks et al. 2016). As air temperatures are consistent over large geographic scales (Schauber et al. 2002), it can be expected that species which use air temperature as a cue for floral initiation will be synchronous in their yearly reproductive effort over similar scales. Koenig and Knops (1998) discovered that significant intraspecific synchrony may occur between populations of northern hemisphere coniferous trees up to 1,000 km apart. High levels of intraspecific synchrony has also been observed in New Zealand species, including species of *Chionochloa* and *Nothofagus*, between populations up to 800 km apart (Schauber et al. 2002). Intraspecific synchrony has not, however, yet been quantified for the species that make up New Zealand's broadleaf-podocarp forests.

As the temperature cues underlying intraspecific synchrony are spatially autocorrelated (Norton and Kelly 1988, Koenig et al. 1999, Koenig and Knops 2000, Schauber et al. 2002), meaning, that they decrease in similarity with increasing distance, it can be expected that intraspecific synchrony will also decrease with increasing distance between populations. This phenomenon has been observed in species of *Abies*, *Chionochloa*, *Nothofagus*, *Picea*, *Pinus*, and *Quercus* (Koenig and Knops 1998, Schauber et al. 2002, Koenig and Knops 2005). Quantification of the rate of decline of intraspecific synchrony is of interest for several reasons. Identifying the rate at which intraspecific synchrony decreases across distance may provide clues as to the specific floral cue for each species. Understanding the spatial extent of intraspecific synchrony may also be used to inform future seed monitoring programs. Species with high levels of intraspecific synchrony may require less spatially intensive seedfall monitoring, when compared to species whose reproductive effort is less synchronous between sites.

Koenig et al. (2003) determined that synchrony between individuals within a population is strongly correlated to the CV of the population. Therefore, if the cues responsible for synchrony within a population are the same cues responsible for synchrony among populations, I hypothesise that there will also be a positive relationship between the intraspecific synchrony of populations and their CV values.

The second form of synchrony, interspecific synchrony, involves the synchrony among species. Understanding the interspecific synchrony within New Zealand's broadleaf-podocarp forests is important in an ecological context, particularly given that the podocarp species are fleshy-fruited and animal-dispersed (Chapter 1: Table 1.3). Synchrony between species is ecologically significant as it determines the total amount of resources available for seed consuming species, particularly generalists than consume the seeds of multiple species. If a species consumes the seeds of two tree species that are non-synchronous or negatively

correlated, the total resource variability will be less than if the tree species were synchronous. This concept is illustrated by figure 3.1.

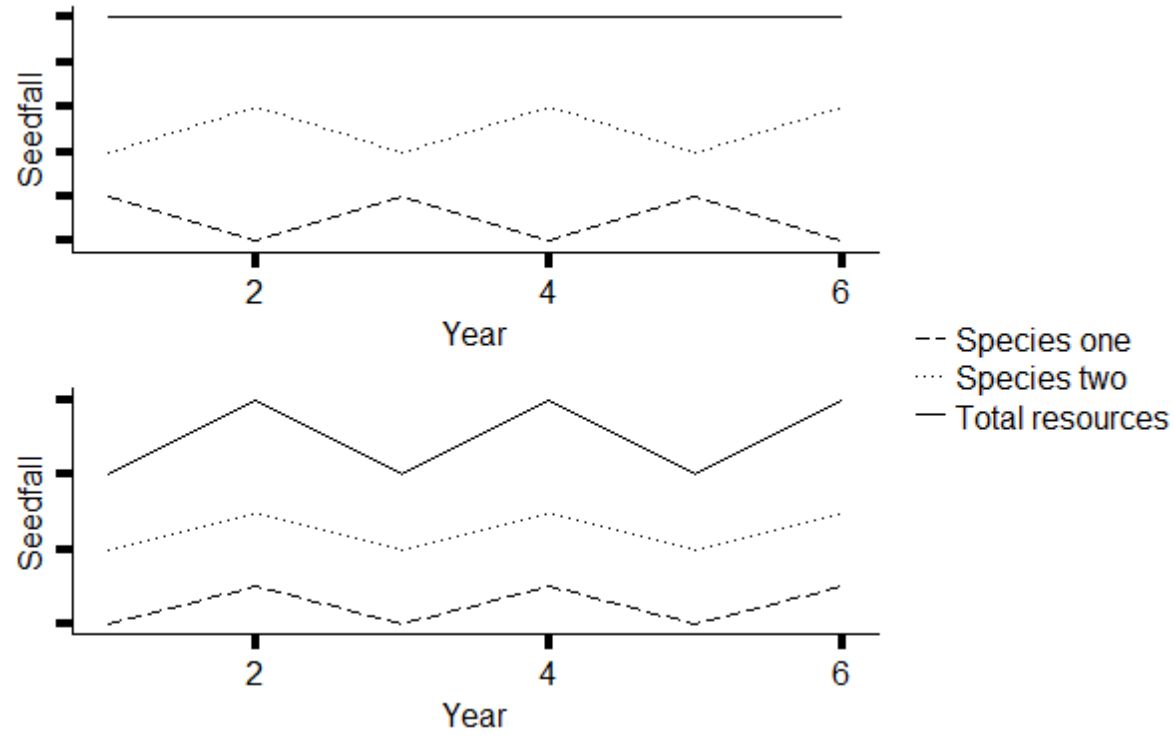

Figure 3.1 The hypothetical effect of two negatively correlated species (top) and two positively correlated (synchronous) species (bottom) on total resource availability for a generalist consumer. Note that because this figure is schematic, units are not included.

Seeds from tree species in broadleaf-podocarp forests are consumed by both native birds (Emeny, Powlesland, Henderson, & Fordham, 2009; Kelly et al., 2010; Williams & Karl, 1996), and introduced mammalian pests (Cowan, 1990; Daniel, 1973). By identifying which species are synchronous, and which are not, we may improve our understanding the resource dynamics occurring in these forests. This information may in turn be used to improve management practices. For example, when organising a potential translocation attempt for a native bird, by knowing the diet of the bird in question, we may determine suitable locations by understanding the synchrony of the trees in the recipient environment, ensuring a consistent food supply.

Schauber et al. (2002) found synchrony to be higher within genera than among genera, although there is currently no consensus on whether this is adaptive (Kelly et al. 2000, Schauber et al. 2002) and is likely situationally dependent. Schauber et al. (2002) suggested that synchrony within and among genera is often due to a paucity of potential floral initiation cues leading to the use of similar cues among species which therefore creates synchronisation of reproductive efforts. It is currently unknown whether this relationship extends to higher taxonomic levels. While tree species within New Zealand's broadleaf-podocarp forests are diverse, from many different genera, they can be taxonomically grouped into two broad categories: angiosperms and gymnosperms. If more closely related species display greater interspecific synchrony of reproduction, this may extend to higher taxonomic groups. It is, therefore, expected that species will display greater synchrony with other species within their taxonomic group than with species from the other taxonomic group.

If synchrony between species does indeed occur due to a paucity of floral initiation cues, as suggested by Schauber et al. (2002), it is expected that species that synchronise large seed events using floral cues (masting species) will be more synchronised with other masting species, than with species whose reproductive effort is determined by localised environmental conditions. Masting intensity, which can be quantified as CV (as described in chapter 2), is therefore expected to have a positive relationship with interspecific synchrony. Similarly, I hypothesise that species that have high levels of intraspecific synchrony, indicating a strong response to a floral initiation cue, will be more synchronous with other species that are highly variable, than with species with low intraspecific synchrony.

In this chapter I aim to quantify and understand both the intraspecific and interspecific synchrony of seed production for species in New Zealand's broadleaf-podocarp forests. To achieve this, I will answer the following questions:

- Does intraspecific synchrony decline with increasing distance between sites?
- Are species that are more variable in their seed production (higher CV) more synchronous between populations?
- Is synchrony higher for pairs of species within angiosperms and gymnosperms than between these groups?
- Do species with higher CVs display greater interspecific synchrony with other species?
- Do species with high intraspecific synchrony also display high interspecific synchrony?

3.2 Methods

Seed data for all analysis in this chapter was prepared using the same methodology described in Chapter 2: 2.2.1 Data checking.

3.2.1 Intraspecific synchrony

To quantify the level of synchrony within species, among sites, pairwise correlations were performed (Bjørnstad et al. 1999, Koenig et al. 1999, Schauber et al. 2002). Pearson r coefficients were calculated for all species that had datasets (described in chapter one) at more than one site. A Pearson r value was calculated for each species for every site pair with at least 4 years of overlap (Table 3.1), on log(+1) transformed data. Therefore, Pearson r coefficients were not calculated for the site combinations of: Okarito-Paengaroa, Okarito-Blue Duck Reserve, and datasets from Cascade Kauri Park were removed completely.

Table 3.1 The number of overlapping sampling years between all site combinations. Only pairs with at least 4 years of overlap were used for correlation calculations.

	Paengaroa	Blue Duck Reserve	Otamatuna	Waipapa	Pelorus Bridge	Okarito	Cascade Kauri Park
Blue Duck Reserve	4						
Otamatuna	5	5					
Waipapa	5	5	8				
Pelorus Bridge	5	5	7	7			
Okarito	2	3	4	4	4		
Cascade Kauri Park	2	2	3	3	3	3	
Trounson Kauri Park	5	5	8	8	7	4	3

A total of eight species met these conditions (Table 3.2), for which, matrices of Pearson r coefficients for all unique site pairs, calculated by pairwise complete observations, were created. For this calculation, the seeds per m^{-2} data was log(+1) transformed as the data was right skewed (positively skewed), a common feature of masting datasets (Norton and Kelly 1988, LaMontagne and Boutin 2009). Using the calculated Pearson r values, one-sample t tests were run to identify which species' mean Pearson r value differed significantly from zero.

Table 3.2 The number of individuals targeted for species with at least two sampling sites and a minimum of five individuals sampled per site. Dashes indicate that less than five individuals were of that species were targeted at that site. Unique site pairs are the number of unique site combinations with at least 4 years of data overlap. Ordered by total unique site pairs.

Species	Blue Duck Reserve	Okarito	Otamatuna	Paengaroa	Pelorus Bridge	Trounson Kauri Park	Waipapa	Unique site pairs
Kahikatea	10	11	-	11	10	6	12	13
Tawa	45	-	23	-	10	5	54	10
Hinau	11	-	10	-	10	-	11	6
Miro	-	10	10	-	10	-	11	6
Rimu	11	-	10	-	5	-	14	6
Matai	15	-	-	7	10	-	13	6
Supplejack	13	-	16	-	-	-	18	3
Totara	11	-	-	-	-	-	10	1
						Total unique species-site pairs:		51

To see how distance affected synchrony, a distance matrix of the distance between every site combination was generated using the geographic information system software QGIS (Team 2012) (Table 3.3). For this calculation each site location was taken as the mean coordinate of all seed traps at the site. Using the calculated Pearson r values of intraspecific synchrony, a GLMM was run to test the effect on intraspecific synchrony of distances between site pairs. For this model, species was used as a random term as the focus of this test was variation in synchrony within species, among sites, rather than variation among species. Linear regressions were also run on all species independently to identify potential species-specific relationships. For this analysis, significance was tested using p values adjusted through Bonferroni correction for multiple comparisons (Abdi 2007).

Table 3.3 Distances (km) between seedfall monitoring sites used in the study. The location of each site was defined as the mean coordinates for seedfall traps used in this study.

	Blue Duck Reserve	Okarito	Otamatuna	Paengaroa	Pelorus Bridge	Trounson Kauri Park
Okarito	312					
Otamatuna	520	799				
Paengaroa	331	609	191			
Pelorus Bridge	106	351	450	258		
Trounson Kauri Park	723	886	425	472	619	
Waipapa	447	699	135	132	360	350

The relationship between intraspecific synchrony and variability of seed production was tested using the previously calculated Person r (3.2.1), and CV (2.2.2) values. Mean Pearson r and CV values were then calculated for each of the eight species with multiple datasets (Table 3.2). Using these values, a linear regression was run to determine the strength and significance of the relationship.

3.2.2 Interspecific synchrony

Interspecific synchrony was calculated for all species pairs that had datasets at the same site. Datasets from Cascade Kauri Park were again excluded from the analysis due to the low number of site years (three). Pearson r values were calculated for each site independently to identify if relationships were consistent across sites. A total of 141 interspecific synchrony values were calculated across all sites, involving 92 unique species pairs. For species pairs with multiple common sites, a Pearson r value was calculated across all common, including all years. This Pearson r value will hereby be referred to as the grand Pearson r value. For all Pearson r calculations were performed using pairwise complete observations on log(+1) transformed seeds per m^{-2} data. Significance of the correlations was tested with significance levels adjusted via Bonferroni correction. Significance was only tested for species pairs with multiple sites as the focus of the study was on relationships that occurred over multiple sites and not on site specific relationships.

Interspecific synchrony was examined to determine whether the taxonomic relationship of the species pairs (angiosperm vs gymnosperm) had a significant effect on their level of synchrony. To test this, every species pair (for which Pearson r values were calculated) was categorised into groups of "within" (angio-angio plus gymno-gymno) and "between" (angio-gymno). A two-sample t test was then run to test for a difference in the mean value of interspecific synchrony.

Using previously calculated Pearson r values for interspecific synchrony and CV (Chapter 2: Table 2.2) values, the relationship between interspecific synchrony and variability of seed production was tested. For this test a single value had to be calculated to summarise the variability of both species in each species pair at each common site. For this purpose, a mean CV value was calculated for each species pair, at each common site. Linear regression was then

run to test for a significant relationship between the mean CV value and the Pearson r value of interspecific synchrony.

3.2.3 Intraspecific synchrony and interspecific synchrony

To test the relationship between intraspecific synchrony and interspecific synchrony, a single value was required for each variable, for every species site pair. For intraspecific synchrony a mean Pearson r value was used. This being, the mean Pearson r value for intraspecific synchrony between the site pair, of both species in the species pair. Species included in this test were, therefore, limited to those with at least a single site pair (Table 3.2). The value for interspecific synchrony was also taken as a mean Person r value. This value was the mean Pearson r value for interspecific synchrony for the species pair at both sites. This method is shown diagrammatically in Figure 3.2.

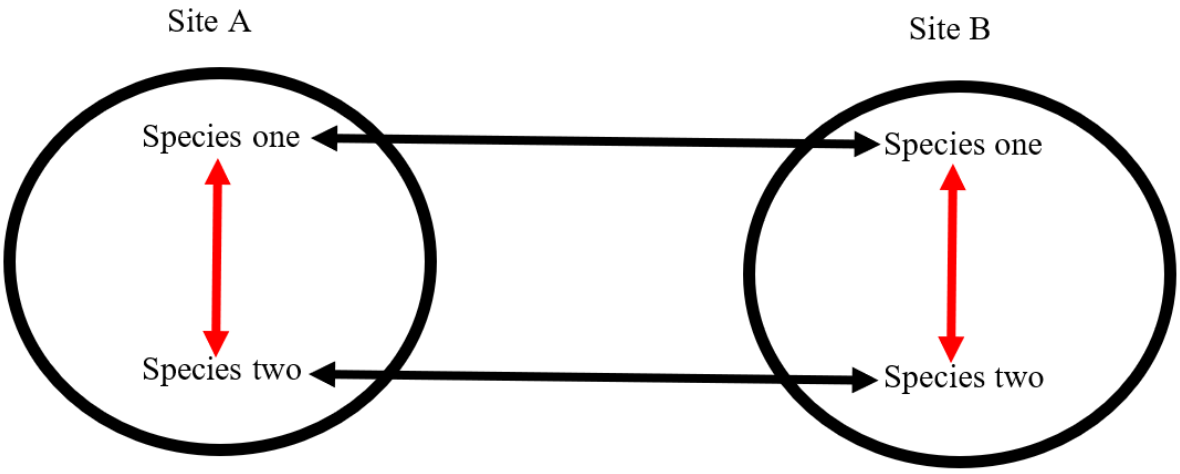

Figure 3.2 Diagrammatic example of a single observation used in the intraspecific~interspecific synchrony study. Each red arrow represents a single interspecific Pearson r value, and each black arrow represents a single interspecific value. Therefore, for a single observation: x = mean of intraspecific Pearson r values, y = mean of interspecific Pearson r values.

3.3 Results

In total I had intraspecific synchrony values for eight species, ranging from a single comparison between two sites (for totara) to 13 pairwise comparisons (for kahikatea). A full list of intraspecific synchrony values, including all species with multiple datasets across all sites (except Cascade Kauri Park), can be found in appendix A. Of the species with multiple site pairs, rimu, kahikatea, hinau and supplejack displayed high levels of synchrony between site pairs (Figure 3.3) with their mean Pearson r values being significantly different from zero (Table 3.4).

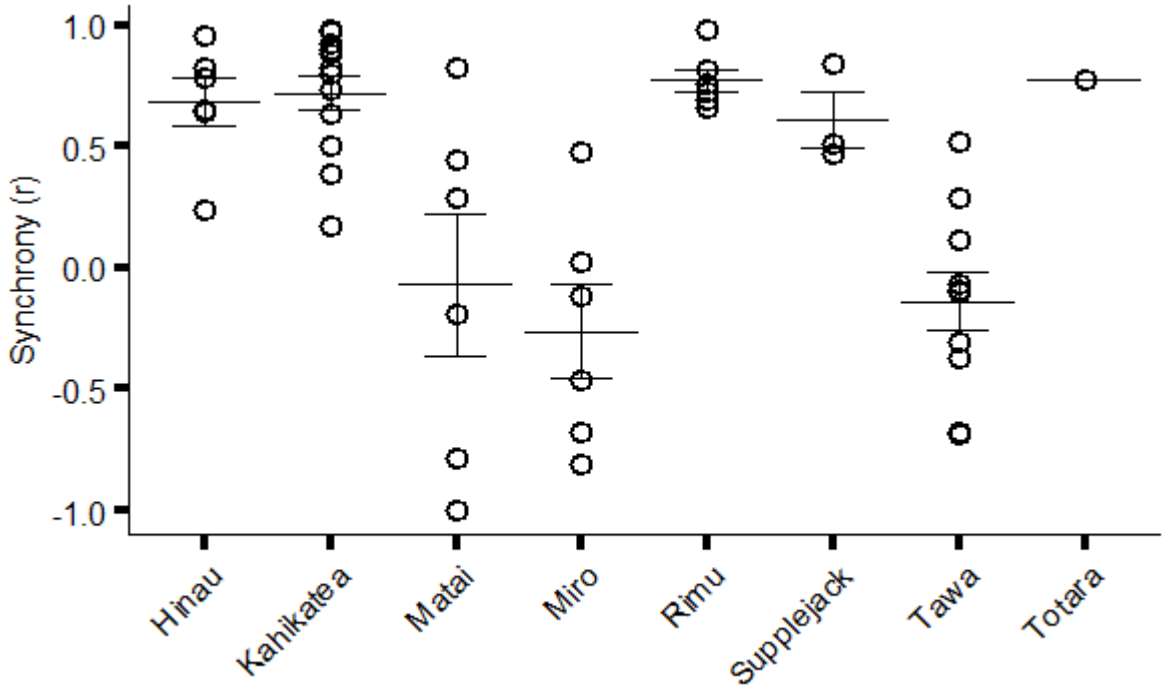

Figure 3.3 The level of synchrony (Pearson r) for the eight study species that have at least two datasets, with a minimum of four years data overlap. The specific site pairs, and the total number of site pairs for each species are given in Table 3.2. All Pearson r values can be found in appendix A. Mean synchrony for each species indicated by the long horizontal lines and the standard error of the mean is indicated by the short horizontal lines. Note that totara only has a single site pair so the large horizontal line is not a mean value.

Matai, tawa, and miro were found to have mean Pearson r values that were not significantly different from zero (Table 3.4) and showed large inconsistency in the level of synchrony between different sites (Figure 3.3). Only one site pair for totara met the criteria for this study (Blue Duck vs Waipapa, with 5 years of overlap). Therefore it was not possible to test whether totara displays significant intraspecific synchrony between sites, although this one pair of sites was highly correlated (Figure 3.3).

Table 3.4 Results of one-sample t tests testing whether species mean levels of synchrony are greater than zero. Ordered by mean Pearson r value. Totara not included due to only having a single site pair.

Species	Mean r	DF	T	P
Rimu	0.77	5	16.26	<0.01
Kahikatea	0.72	12	10.56	<0.01
Hinau	0.68	5	6.72	<0.01
Supplejack	0.61	2	5.18	0.04
Matai	-0.07	5	-0.23	0.82
Tawa	-0.14	9	-1.12	0.29
Miro	-0.26	5	-1.34	0.24

The results of the GLMM identified no significant relationship between the distance between sites, and the intraspecific synchrony of species at the sites, while controlling for species ($F(1,43.46) < 0.01$, $p = 0.99$, R^2 marginal <0.01, R^2 conditional = 0.55) (Figure 3.4). Independent regression analyses of the species with multiple site pairs identified a single species, rimu, to significantly decrease in intraspecific synchrony with increasing distance between sites (Table 3.5, Figure 3.4). While this relationship gave a good fit (R^2=0.75), the regression slope was not steep and the result was not significant after Bonferroni correction for multiple comparisons (Table 3.5).

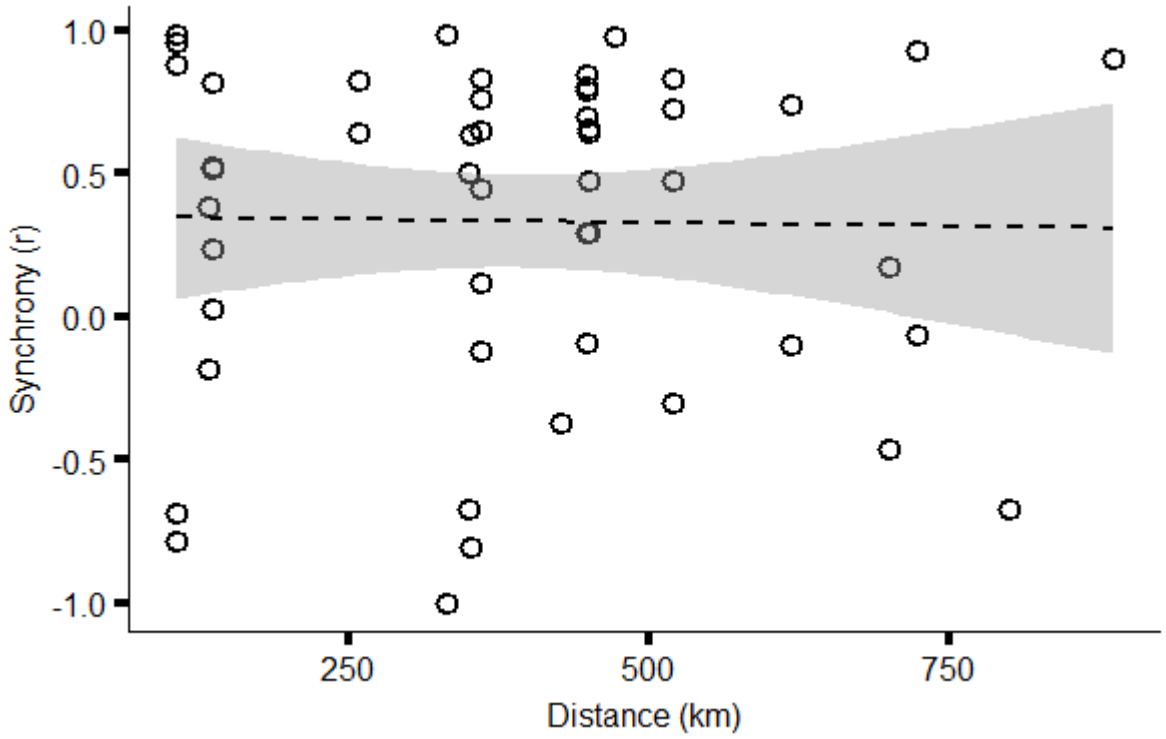

Figure 3.4 The relationship between intraspecific synchrony (Pearson r) and the distance between sites, for the seven species with multiple site pairs (Table 3.2). Note that the random term (species) from the GLMM cannot be visualised by this scatterplot. Nonsignificant linear model represented by the dashed line with standard error included.

Table 3.5 Results of regression analysis on individual species for the relationship between intraspecific synchrony and distance between site pairs, ordered by quality of fit (R^2). Adjusted p-values calculated using Bonferroni correction for multiple comparisons.

Species	DF	F Value	P	P (adjusted)	R^2
Rimu	1,4	11.72	0.03	0.19	0.75
Supplejack	1,1	0.07	0.84	1.00	0.06
Matai	1,4	0.63	0.47	1.00	0.14
Hinau	1,4	0.32	0.60	1.00	0.07
Kahikatea	1,11	0.09	0.77	1.00	0.01
Miro	1,4	0.83	0.41	1.00	0.17
Tawa	1,8	0.02	0.89	1.00	<0.01

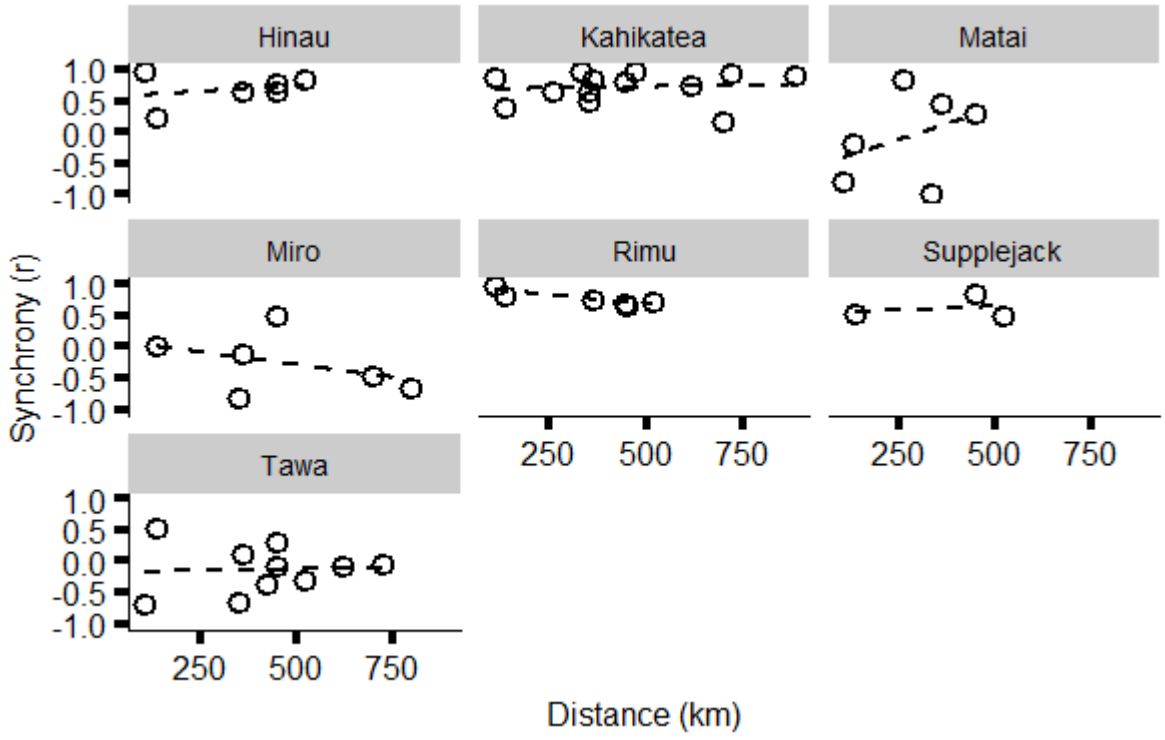

Figure 3.5 The relationship between intraspecific synchrony (Pearson r) and the distance between sites for all species with more than one site pair. Non-significant linear model for each species represented by the dashed lines.

Linear regression identified no significant relationship between species variability of interannual seed production and intraspecific synchrony ($F(1,6) = 1.25$, $p = 0.31$), with the model providing a poor fit ($R^2 = 0.17$). The study species appear to fall into two distinct groupings: high synchrony species and low synchrony species. As shown by the error bars of Figure 3.3, matai, miro, and tawa were not significantly different in their level of intraspecific synchrony, while being significantly different from the remaining study species.

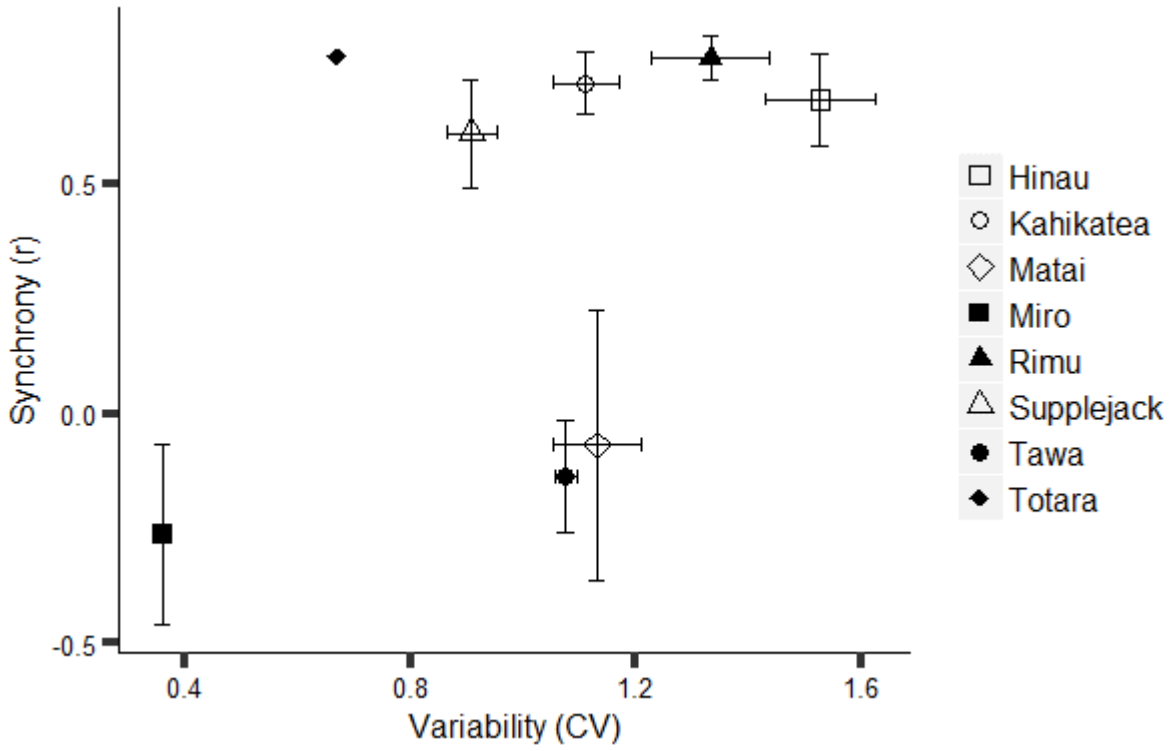

Figure 3.6 The relationship between variability of interannual seed production (calculated as mean CV value across all sites for each species), and intraspecific synchrony (calculated as a mean value for site pairs for each species). Standard error bars for these calculations included. Error bars are not present for totara as it was only sampled at two sites and therefore only one Pearson r, and one mean CV value were calculated. Note that miro was so consistent in its variability of seed production across sites (standard error = 0.01), that the x-axis error bars are not visible at this scale.

3.3.1 Interspecific synchrony

The results in this section have been separated into species pairs with multiple common sites (Table 3.6a), and species pairs with a single common site (Table 3.6b). Having more replicates (common sites) increases validity of the assessment, as it makes it possible to identify which relationships occur over multiple sites, and which are site specific. The level of interspecific synchrony for species pairs with multiple common sites (Table 3.6a) has been presented as both a mean Pearson r value for all common sites, and a grand Pearson r value for this reason. By including a mean Pearson r value it was possible to calculate the standard error, indicating the consistency of the relationship over all common sites. A full list of site-wise Pearson r values for all species pairs can be found in appendix B.

Table 3.6a Mean Pearson r values for species pairs with at least two common sites. p values presented to two decimal places with significant values (α = 0.05) in bold. Both p values relate to the significance of the grand Pearson r value. p adjusted = p value adjusted by Bonferroni correction. Table ordered by grand Pearson r value.

Species one	Species two	Grand Pearson r	p	p adjusted	Mean Pearson r	Standard error	Total sites	Total years (n)
Hinau	Totara	0.69	**0.01**	0.36	0.77	0.10	2	12
Kahikatea	Totara	0.59	**0.04**	1.00	0.66	0.01	2	12
Hinau	Kahikatea	0.57	**0.01**	0.31	0.61	0.15	3	19
Rimu	Totara	0.57	0.06	1.00	0.75	0.14	2	12
Miro	Rimu	0.56	**<0.01**	0.15	0.67	0.09	3	23
Rimu	Supplejack	0.53	**0.02**	0.46	0.62	0.20	3	20
Kahikatea	Miro	0.50	**0.03**	0.75	0.49	0.18	3	19
Tawa	Totara	0.46	0.13	1.00	-0.27	0.65	2	12
Supplejack	Tawa	0.43	0.06	1.00	0.31	0.43	3	20
Kahikatea	Supplejack	0.42	0.18	1.00	0.34	0.14	2	12
Kahikatea	Tawa	0.41	**0.03**	0.89	0.04	0.33	4	27
Matai	Tawa	0.38	0.11	1.00	-0.10	0.42	3	19
Miro	Supplejack	0.36	0.17	1.00	0.26	0.20	2	16
Hinau	Rimu	0.30	0.13	1.00	0.57	0.12	4	27
Supplejack	Totara	0.26	0.41	1.00	0.54	0.27	2	12
Hinau	Tawa	0.26	0.19	1.00	-0.14	0.28	4	27
Hinau	Supplejack	0.24	0.30	1.00	0.49	0.12	3	20
Kahikatea	Rimu	0.23	0.35	1.00	0.56	0.10	3	19
Hinau	Matai	0.03	0.89	1.00	0.07	0.50	3	19
Miro	Tawa	0.01	0.97	1.00	0.29	0.14	3	23
Kahikatea	Matai	-0.01	0.95	1.00	-0.06	0.33	4	24
Matai	Supplejack	-0.06	0.85	1.00	0.13	0.36	2	12
Matai	Totara	-0.14	0.67	1.00	0.22	0.53	2	12
Matai	Miro	-0.20	0.48	1.00	-0.09	0.08	2	15
Rimu	Tawa	-0.21	0.29	1.00	-0.01	0.28	4	27
Hinau	Miro	-0.23	0.28	1.00	0.04	0.17	3	23
Matai	Rimu	-0.45	0.06	1.00	-0.12	0.36	3	19

Table 3.6b Pearson r values for species pairs with a single common site pair. Table ordered by Pearson r value.

Species one	Species two	Pearson r	Monitoring site	Years (n)
Kahikatea	Mountain Beech	>0.99	Blue Duck Reserve	4
Kahikatea	Lowland ribbonwood	0.98	Paengaroa	5
Mahoe	Tawa	0.97	Blue Duck Reserve	4

Matai	Mountain Beech	0.90	Blue Duck Reserve	4
Rimu	Tawari	0.82	Otamatuna	8
Hinau	Mountain Beech	0.81	Blue Duck Reserve	4
Kahikatea	Needle-leaved totara	0.80	Okarito	4
Red Beech	Supplejack	0.79	Otamatuna	8
Red Beech	Tawa	0.75	Otamatuna	8
Hinau	Red Beech	0.73	Otamatuna	8
Red Beech	Tawari	0.70	Otamatuna	8
Tawa	Tawari	0.64	Otamatuna	8
Mountain Beech	Totara	0.61	Blue Duck Reserve	4
Coprosma grandifolia	Matai	0.59	Paengaroa	5
Supplejack	Tawari	0.59	Otamatuna	8
Red Beech	Rimu	0.55	Otamatuna	8
Miro	Totara	0.55	Waipapa	8
Coprosma grandifolia	Hoheria sp	0.50	Paengaroa	5
Black Maire	Coprosma grandifolia	0.47	Paengaroa	5
Kohekohe	Taraire	0.47	Trounson Kauri Park	8
Miro	Tawari	0.46	Otamatuna	8
Mountain Totara	Tawari	0.46	Otamatuna	8
Black Maire	Matai	0.45	Paengaroa	5
Hoheria sp	Pittosporum sp	0.41	Paengaroa	5
Hinau	Tawari	0.41	Otamatuna	8
Black Maire	Kahikatea	0.39	Paengaroa	5
Miro	Mountain Totara	0.33	Otamatuna	8
Kauri	Taraire	0.32	Trounson Kauri Park	8
Mountain Beech	Rimu	0.29	Blue Duck Reserve	4
Mountain Totara	Supplejack	0.25	Otamatuna	8
Mountain Totara	Red Beech	0.24	Otamatuna	8
Black Maire	Lowland ribbonwood	0.22	Paengaroa	5
Hoheria sp	Matai	0.22	Paengaroa	5
Mountain Totara	Tawa	0.18	Otamatuna	8
Kahikatea	Kohekohe	0.15	Trounson Kauri Park	8
Mountain Beech	Supplejack	0.15	Blue Duck Reserve	4
Mountain Totara	Rimu	0.14	Otamatuna	8
Black Maire	Hoheria sp	0.13	Paengaroa	5
Miro	Red Beech	0.06	Otamatuna	8
Taraire	Tawa	0.03	Trounson Kauri Park	8
Miro	Needle-leaved totara	0.00	Okarito	4
Lowland ribbonwood	Pittosporum sp	-0.02	Paengaroa	5
Kauri	Kohekohe	-0.07	Trounson Kauri Park	8
Kahikatea	Taraire	-0.16	Trounson Kauri Park	8
Kahikatea	Pittosporum sp	-0.22	Paengaroa	5
Coprosma grandifolia	Kahikatea	-0.29	Paengaroa	5
Kahikatea	Kauri	-0.31	Trounson Kauri Park	8
Kohekohe	Tawa	-0.35	Trounson Kauri Park	8
Hinau	Mountain Totara	-0.37	Otamatuna	8

Coprosma grandifolia	Lowland ribbonwood	-0.48	Paengaroa	5
Kauri	Tawa	-0.53	Trounson Kauri Park	8
Black Maire	Pittosporum sp	-0.55	Paengaroa	5
Coprosma grandifolia	Pittosporum sp	-0.55	Paengaroa	5
Hoheria sp	Kahikatea	-0.55	Paengaroa	5
Hoheria sp	Lowland ribbonwood	-0.56	Paengaroa	5
Matai	Pittosporum sp	-0.56	Paengaroa	5
Mahoe	Supplejack	-0.58	Blue Duck Reserve	4
Lowland ribbonwood	Matai	-0.67	Paengaroa	5
Mahoe	Rimu	-0.69	Blue Duck Reserve	4
Mahoe	Totara	-0.87	Blue Duck Reserve	4
Mountain Beech	Tawa	-0.88	Blue Duck Reserve	4
Mahoe	Mountain Beech	-0.89	Blue Duck Reserve	4
Kahikatea	Mahoe	-0.92	Blue Duck Reserve	4
Mahoe	Matai	-0.97	Blue Duck Reserve	4
Hinau	Mahoe	-0.98	Blue Duck Reserve	4

Of the species pairs with multiple common sites, 7/27 (26%) were significant prior to Bonferroni correction. However, a post hoc Chi square goodness of fit test identified the that the number of significant results prior to Bonferroni correction (7/27) to be higher than expected $X^2(1, N = 27) = 24.89$, $p < 0.001$. The strongest relationship observed across multiple sites was between hinau and totara (grand Pearson $r = 0.69$, $n = 12$, Table 3.6a). Some species pairs, such as miro and rimu, displayed consistent positive relationships across all sites (Figure 3.7).

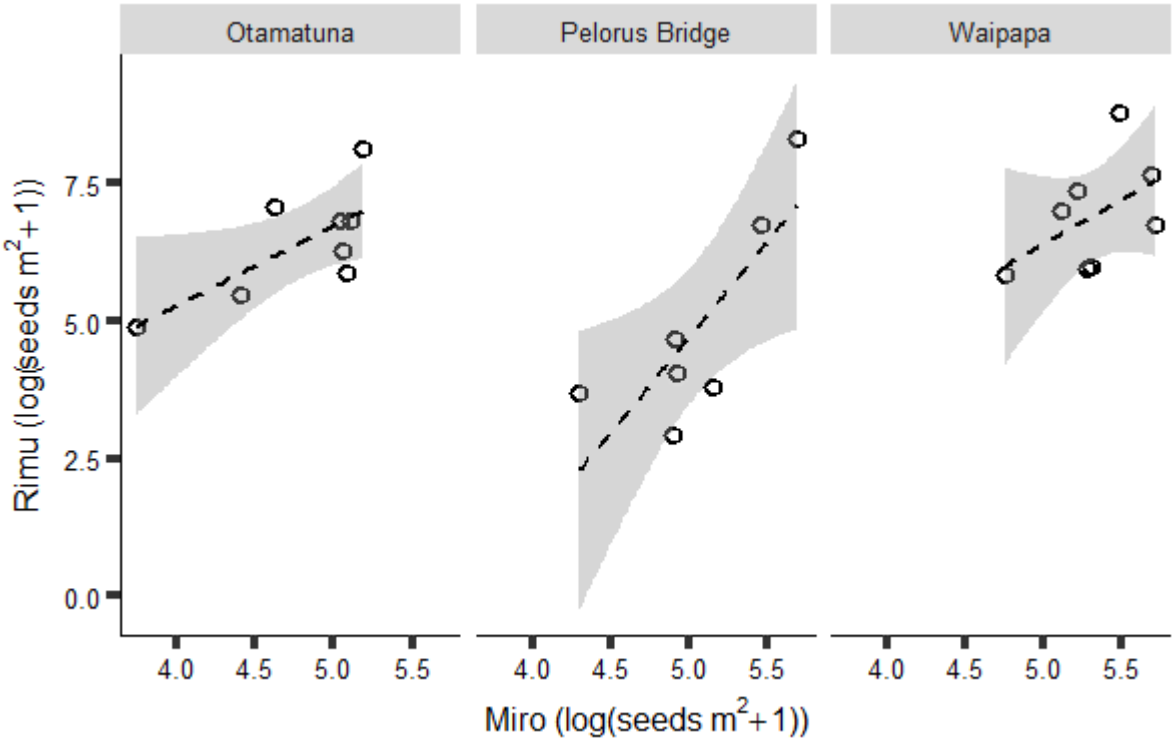

Figure 3.7 The relationship between miro and rimu across their three common sites. Dashed line indicates the non-significant linear models, standard error included. Pearson r: 0.72 (Otamatuna), 0.81 (Pelorus Bridge), 0.50 (Waipapa).

However, other species pairs displayed inconsistency in their relationships among sites, identified by their large standard errors of mean Pearson r values (Table 3.6a). The relationship between matai and hinau was particularly inconsistent, displaying positive synchrony at Blue Duck Reserve, negative synchrony at Pelorus Bridge, and almost no relationship at Waipapa (Figure 3.8)

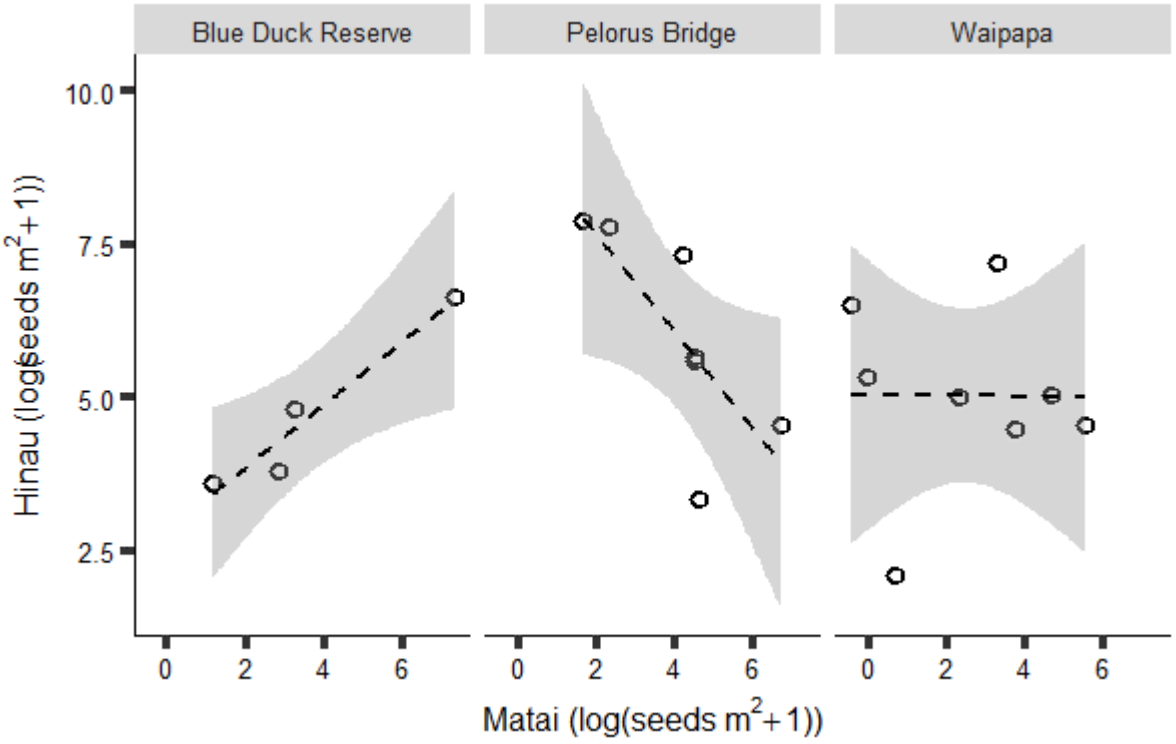

Figure 3.8 The relationship between matai and hinau across their three common sites. Dashed line indicates the non-significant linear models, standard error included. Pearson r: 0.97 (Blue Duck Reserve), -0.76 (Pelorus Bridge), <0.01 (Waipapa).

Species combinations with less than three common sites showed greater extremes in their interspecific synchrony of seed production (Table 3.b). Of these species combinations, the relationship between kahikatea and mountain beech at their single common site (Blue Duck Reserve) was the most extreme, with the species displaying near perfect synchrony over the four sample years (Figure 3.9, left). Conversely, a near perfect negative relationship was observed between hinau and mahoe, also occurring at their only common site; Blue Duck Reserve (Figure 3.9, right).

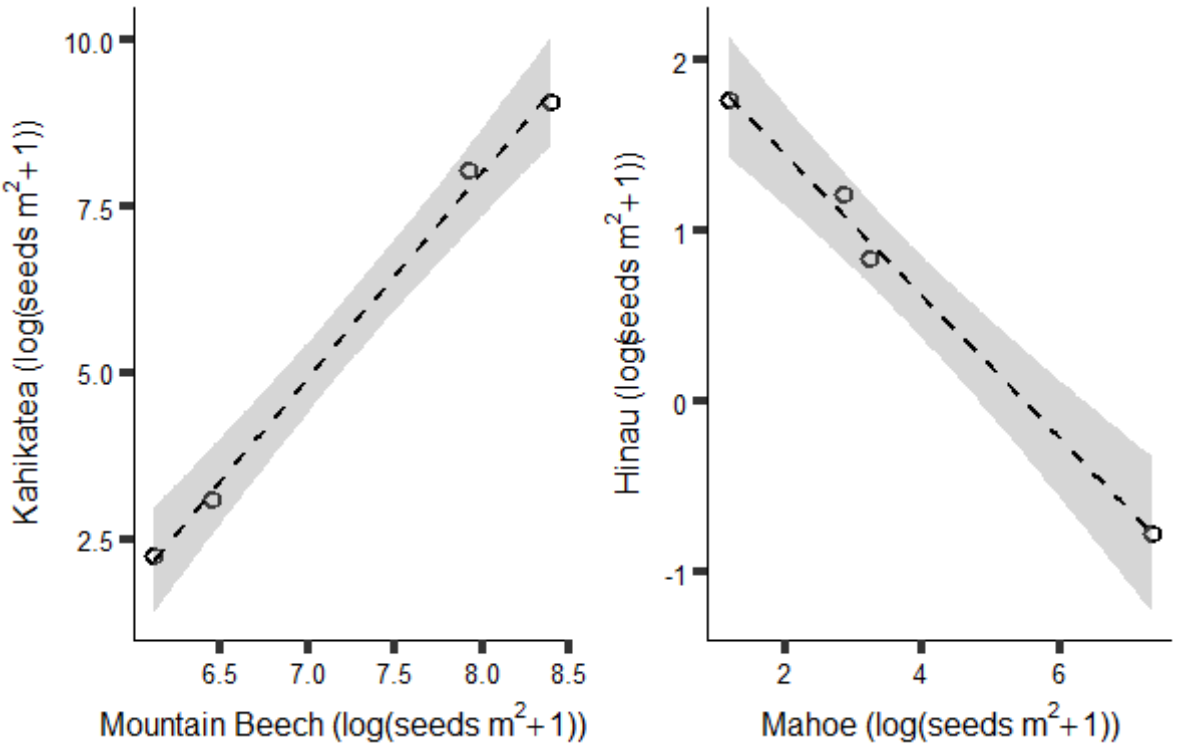

Figure 3.9 ***Left:*** *The relationship between the most positively synchronous species pair (Kahikatea - Mountain Beech, r > 0.99) at their single common site; Blue Duck Reserve.* ***Right:*** *The relationship between the most negatively synchronous species pair (Hinau-Mahoe, r = -0.98) at their single common site; Blue Duck Reserve. Linear models for which significance was not tested are included, as well as standard error.*

Mean interspecific synchrony was greatest between species from the same high-level taxonomic group compared to between species from different high-level taxonomic groups (Figure 3.10). However, the difference was not significant (t = 0.49, df = 136.02, p = 0.62). High levels of synchrony, and strong negative correlations, were observed both within and between the high-level taxonomic groups.

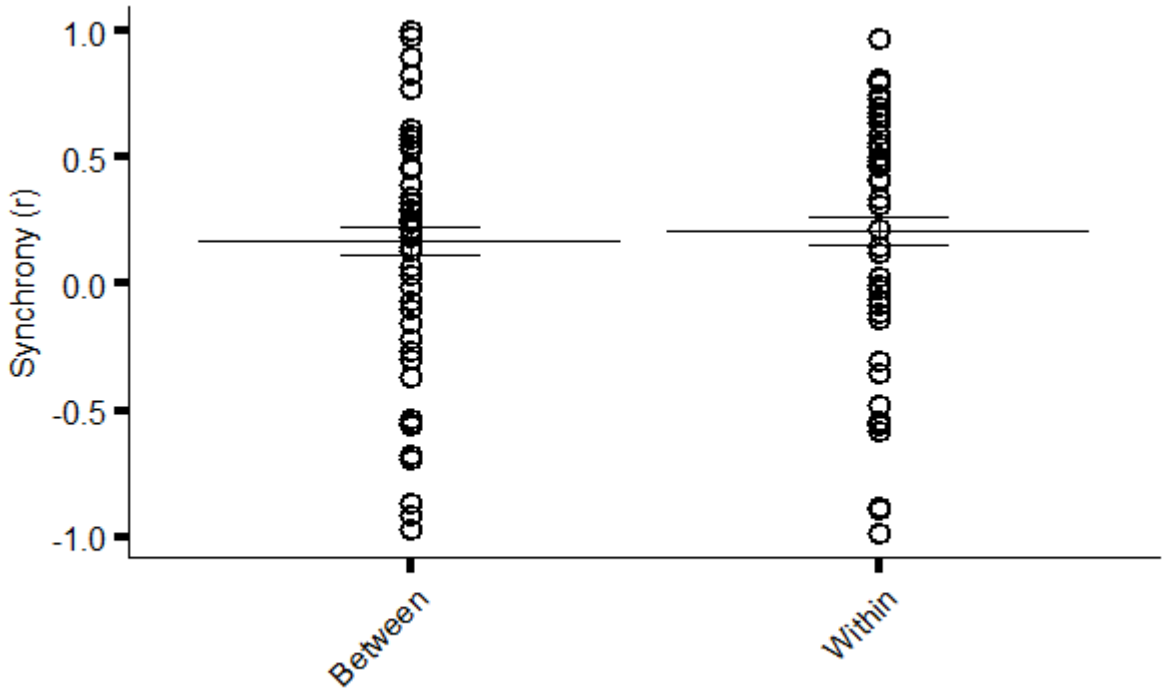

Figure 3.10 Interspecific synchrony (Pearson r) for every species pair (including all sites except Cascade Kauri Park) grouped by whether each species in the pair is in the same high-level taxonomic group (Within = Angio-angio plus gymno-gymno) or from different high-level taxonomic groups (Between = angio-gymno). Wide horizontal lines represent the mean for each group which are: Between = 0.17±0.05, within = 0.21±0.05.

No significant relationship was identified between the level of synchrony between two species at a site and the mean CV value of these species at this site (F value (1,139) = 1.98, p = 0.16). The linear model provided a poor fit, with mean variability of species pairs explaining very little of the observed variance in interspecific synchrony (R^2 = 0.01, Figure 3.11).

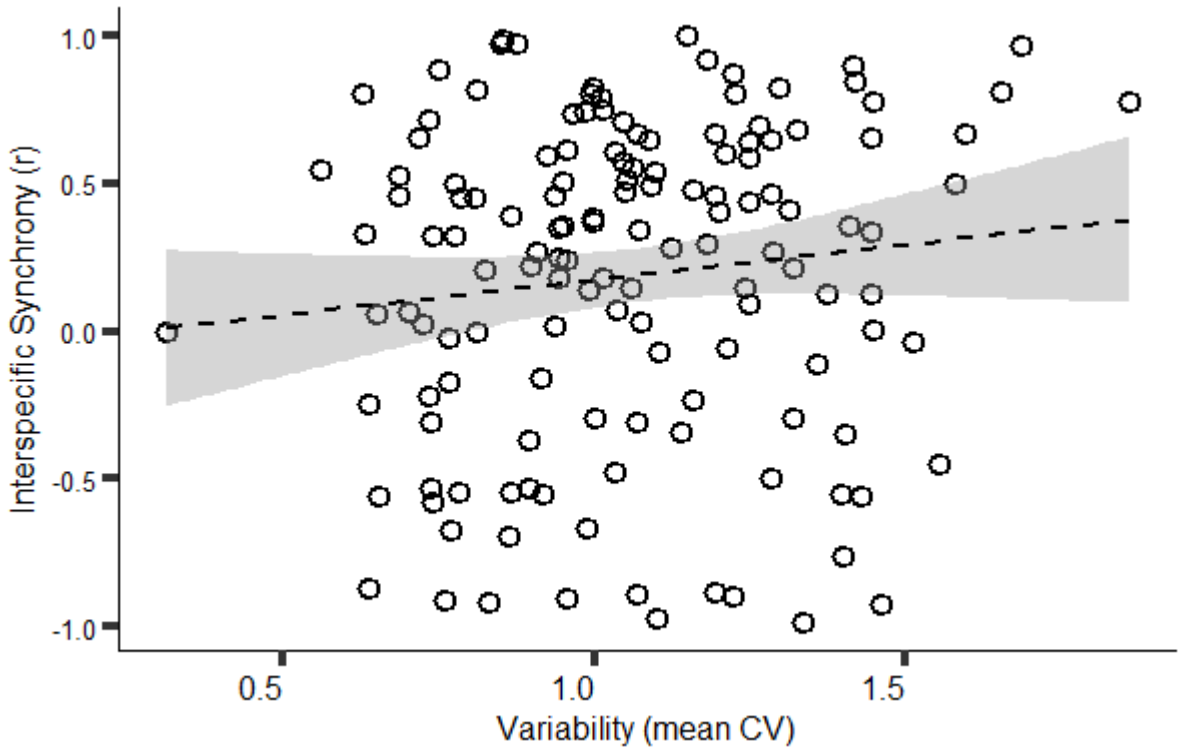

Figure 3.11 The relationship between interspecific synchrony of species pairs and the mean CV of species pairs at each site. Non-significant linear model represented by the dashed line with standard error included.

3.3.2 Intraspecific synchrony and interspecific synchrony

Intraspecific synchrony was identified as having a significant relationship with interspecific synchrony (F value (1,74) = 21.31, $p < 0.01$, $R^2 = 0.22$). Pairs of species that were highly synchronous with themselves between two sites (high mean intraspecific synchrony), were more highly synchronous with each other at the two sites (high mean interspecific synchrony) (Figure 3.12).

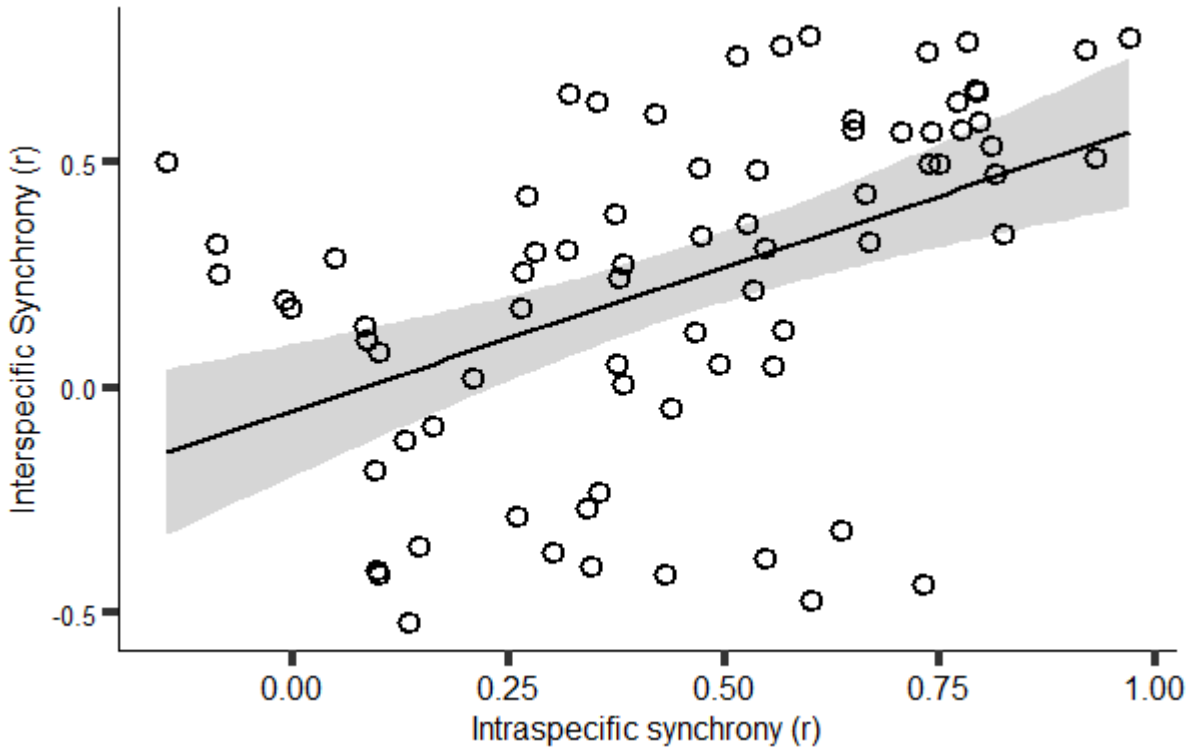

Figure 3.12 The relationship between the mean level of intraspecific synchrony for a species pair at a site pair, and the mean level of interspecific synchrony for these species for the sites. Significant linear model represented by the solid line and standard error bars included.

While the linear model proved to be significant, it appeared as if the direction of the relationship shifts when the mean interspecific synchrony for a species pair is below zero (i.e. negative correlation). Consequently, the data was separated post hoc into negative and positive mean interspecific synchrony species pairs. Separating the data in such away improved the fit of the model for positive interspecific synchrony species pairs (F value (1,55) =26.62, $p < 0.01$, $R^2 = 0.33$) (Figure 3.12: left). For species pairs with a negative mean interspecific synchrony (Figure 3.12: right) there the slope of the relationship was negative, however the model provided a poor fir and was not significant (F value (1,17) =1.69, p =0.21, $R^2 = 0.09$).

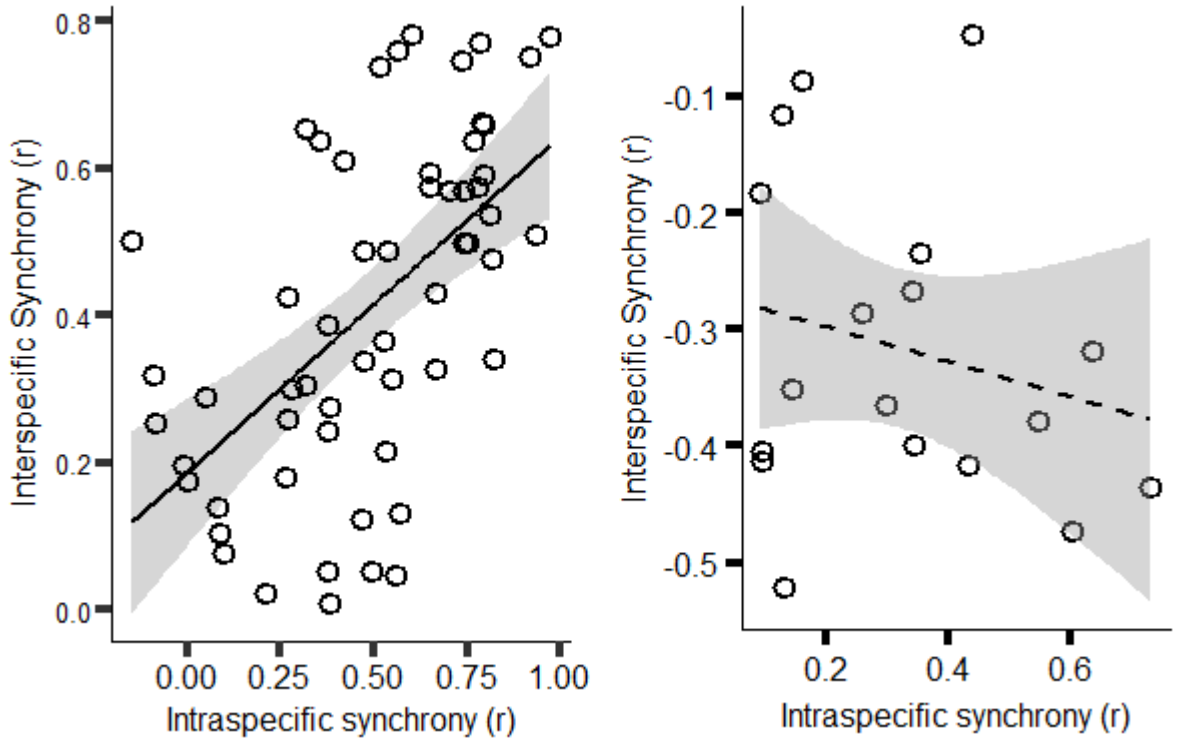

Figure 3.13 The relationship between the mean level of intraspecific synchrony for a species pair between a pair of sites, and the mean level of interspecific synchrony for these species over these two sites. ***Left****: only species pairs with positive mean interspecific synchrony at the site pairs. Significant linear model (solid line) and standard error bars included.* ***Right****: only species pairs with negative mean interspecific synchrony at the site pair. Non-significant linear model (dashed line) and standard error bars included.*

3.4 Discussion

3.4.1 Intraspecific synchrony

Synchronisation of reproductive efforts by spatially separate populations of plants have previously been observed in a wide range of species (Koenig et al. 1994, Koenig et al. 1999, Kelly et al. 2000, Schauber et al. 2002). However, until now little was known about the intraspecific synchrony among populations of species that make up New Zealand's broadleaf-podocarp forests. I have identified four species in New Zealand's broadleaf-podocarp forests that are significantly synchronous between populations, even over large geographic ranges (rimu, kahikatea, hinau, and supplejack). Rimu displayed high levels of synchrony over all populations (all population combinations $r > 0.65$, Appendix A), despite distances between

populations ranging up to 520 km. While rimu has been found to synchronous between populations before, this is the first time it has been reported on such spatial scales (Schauber et al. 2002). Kahikatea was also highly synchronous between distant populations, with its most distant populations (886 km apart) displaying nearly perfect synchrony (r = 0.9). To my knowledge, this is the first time populations of kahikatea have been shown to be synchronous over any spatial scales. Intraspecific synchrony over large geographic distances are, however, not unique to the species in the current study. Spatial synchrony on comparable scales has been previously observed in species of California oak (genus *Quercus*), beech (genus *Fagus*), and several northern hemisphere coniferous trees (Koenig and Knops 1998, 2000, Yasaka et al. 2003, Koenig and Knops 2013).

It has previously been observed that synchrony relationships often decrease in strength linearly with increasing distance between populations. This has been shown for within-genus synchrony for species of *Chionochloa* and *Nothofagus* (Schauber et al. 2002). Koenig and Knops (2000) also describe a similar relationship within several taxa, with study species including conifers and broadleaf species. This relationship was not, however, found in the current study. The absence of this relationship may be due a combination of the underlying mechanisms of population synchrony, the scale of the study, and the geographic locations of the study sites.

Synchrony of reproductive efforts between individual plants has been attributed to either pollen movement and/or synchronous environmental forcing (Liebhold et al. 2004b). While pollen movement (where proximity of individuals is linked to pollen exchange and synchrony of seed production) may explain spatial synchrony within a population (Satake and Iwasa 2002), it cannot explain population level synchrony between distant populations, as observed in the current study. Synchronous environmental forcing, also known as the Moran effect (Moran 1953), states that synchrony of geographically separate populations may occur

through the synchrony of environmental influences. The selective and adaptive trait of masting is built upon this concept. Species that perform "mast seeding" are believed to achieve high levels of synchrony between individuals using external synchronising cues. Studies have identified that for many species, this cue often relates in some way to the temperature preceding or during floral induction (i.e. summer air temperatures) (Norton and Kelly 1988, Kelly et al. 2013, Monks et al. 2016). It is likely that the species with high synchrony between sites in the current study (rimu, kahikatea, hinau, and supplejack) use similar external cues to achieve their high level of synchrony. While little is known about the synchronising cues for most of the species in the current study, variation in rimu seed production has been previously associated with summer air temperatures (Norton and Kelly 1988). It may be that the external synchronising cues for these species do not change over scales detectable within the current study range. While Koenig and Knops (2000) found significant reductions in intraspecific synchrony over distance, synchrony only consistently reduced across their study species once monitoring sites were between 500 km to 1000 km apart. For the current study, this represents the upper range of inter-site distance, with only 12/51 (23.5%) of calculated intraspecific synchrony values occurring between sites >500 km apart. Therefore, the sampling design of the current study (which is constrained by the geographic extent of the New Zealand land mass) may have limited my ability to detect changes in synchrony if synchronising cues are consistent over larger spatial scales than the study range.

Alternatively, the hypothesis that a species' intraspecific synchrony should decline linearly with distance relies on the assumption that the synchrony of floral cues for each species also decline linearly with distance. This may be a flawed assumption. Distance is an imperfect proxy for environmental similarity, as it fails to incorporate known relationships between local geography and weather. Regional temperature differences in New Zealand have been shown to be associated with factors including altitude, latitude, distance to the nearest coast, and regional

sea surface temperatures (Norton 1985, Basher and Thompson 1996). Distance between sites does not directly capture changes in these variables, therefore, it cannot be expected to fully predict the breakdown of synchrony in weather based floral cues. A better approach might be to use direct measurements of local temperatures to see if seedfall synchrony is related to similarity of weather. Schauber et al. (2002) demonstrated that temperature similarity between sites provided a better fit with intraspecific synchrony in *Chionochloa* and *Nothofagus*, compared to distance between sites.

As for the low-synchrony species in the study, these being matai, tawa, and miro, the absence of a relationship between synchrony and distance may be due to them lacking a synchronising cue. Individuals of species that do not gain a selective and adaptive advantage from mast seeding are likely to not synchronise their reproductive effort using external cues. In fact, in the absence of selective benefits, synchrony between individuals may reduce reproductive efficiency through lost colonisation opportunities and increased density-dependent mortality (Hett 1971, Waller 1979). Without a synchronising cue it would be expected that these species would have low intraspecific synchrony between populations and form no relationship with distance as reproductive effort would reflect localised environmental conditions.

While I predicted that species with high CV values would be more synchronised among sites (within species), as local synchronising cues may be conserved over large areas, this hypothesis was not supported. Instead, it was discovered that species form two distinct groups, these being species with high levels of synchrony between populations, and those with low levels of synchrony between populations. This separation likely indicates which species have floral cues that are consistent over large geographic areas and those which either lack strong floral initiation cues or have cues that are highly localised. That may reflect selection for synchrony (i.e. mast seeding) in some species but not in others. The lack of relationship

between CV and intraspecific synchrony may also be due to the indirect relationship of floral cues with population level variability. As population level variability of seed production is the product of variability of individuals and the synchrony between individuals (Herrera 1998), a species may respond strongly to a floral cue (i.e. high synchrony between individuals, and subsequently between populations) yet exhibit a low CV if individuals within the population are not highly variable in their seed production. Furthermore, Koenig et al. (2003) identified that variability of individuals within a population plays a larger role in determining a populations CV than the synchrony between these individuals. Species with high synchrony between individuals but with low individual level variability may therefore further contribute to the lack of relationship between intraspecific synchrony and variability of seed production.

3.4.2 Interspecific synchrony

While none of the interspecific relationships were found to be significant (after Bonferroni correction), strong correlations between species' interannual seed production effort was observed. Lack of significant relationships is likely due to a combination of factors, both statistical and biological. Seven species pairs were significant prior to Bonferroni correction (Table 3.6), however, the large number of species relationships tested in the study rendered these relationships non-significant after Bonferroni correction. While Bonferroni correction is a conservative approach (Abdi 2007), it is necessary to allow for the statistically expected increase in the number of type I errors (false positives) associated with multiple comparisons. Consequently, this correction is likely to increase the number of type II errors (false negatives). It is, therefore, expected that some of the species pairs that demonstrated significant synchrony prior to Bonferroni correction truly are significantly correlated in their interannual effort of seed production. This was supported by the significant chi square goodness of fit test, indicating that the number of observed significant correlations was significantly more than expected. While it was not possible to statistically identify significant synchrony relationships

in the current study, these datasets are ongoing, and the sample size (number of years) for these correlations increasing. Therefore, the datasets will be better suited to detection of significant interspecific relationships in future studies.

The current study has highlighted the importance of replication, in terms of the number of sampling sites, for such future studies. It was observed that interspecific relationships may vary in their strength and direction, depending on the location of the populations in question. In the current study, matai and hinau were found to have a strong correlation in their yearly seedfall at Blue Duck Reserve (Pearson r = 0.97, Figure 3.8). If this was the only sampling location for these species it may be tempting to conclude that they share a common floral cue. However, this relationship was not consistent across the other sampling locations (Figure 3.8). Location-specific relationships likely indicate that the species do not share a common floral cue, but instead, may have floral cues that covary to different degrees depending on local environmental factors. Hence, I stress the importance of obtaining data from as many locations as possible for future studies of interspecific relationships. The DOC seedfall network will also allow increasingly powerful tests of synchrony as more years of data accumulate, since chance relationships will become less likely as a greater number of years are included in each comparison.

Species' synchrony of seed production varied greatly in strength, with both positive, and negative correlations identified in the current study. As predicted, species from the same high-level taxonomic group were more synchronous than between high-level taxonomic groups. However, the difference in mean interspecific synchrony between this group was nonsignificant. While synchrony between closely taxonomically related species (within-genus) has been previously shown to be higher than more distantly related species (between genera) (Schauber et al. 2002), taxonomic relation at a very high level was not a significant factor in my analysis. This is likely due to the vastly different levels of taxonomic relation. Species

belonging to angiosperms and gymnosperms are diverse, both within and between these groups. While angiosperms are monophyletic (with members belonging to a single phylum: Anthophyta), gymnosperms are polyphyletic (with members belonging to three phyla: Coniferophyta, Ginkgophyta, and Gnetophyta), however, it should be noted that all the gymnosperms in the current study belong to same phylum, Coniferophyta. Phylum is a very high taxonomic distinction compared to genus, therefore, the members of these phyla are, on average, much less closely related than within a genus. Evolution of the masting trait, specifically the floral cue responsible for synchrony, is therefore less likely to be consistent across a phylum than within a genus.

3.4.3 Interspecific synchrony and intraspecific synchrony

As hypothesised, species with higher levels of synchrony between populations displayed higher levels of interspecific synchrony. This is likely due to high intraspecific synchrony indicating the use of one or two simple external cues for floral initiation and synchronisation of large reproductive efforts, as opposed to simple reproductive responses to fluctuating localised environmental conditions across all environmental variables. If two species use floral cues to synchronise their reproductive efforts within each species, there is a heightened chance of synchrony between the species owing to the limited number of potential floral cues (Webb and Kelly 1993). Furthermore, for many New Zealand species the synchronising cue has been found to often relate to warm summer temperatures (Norton and Kelly 1988, Webb and Kelly 1993, Kelly et al. 2000, Kelly et al. 2013, Monks et al. 2016).

Post-hoc separation of species site-pairs into positive and negative mean interspecific synchrony values strengthened the relationship between intraspecific synchrony and interspecific synchrony for positively related species pairs. However, no relationship between intraspecific synchrony and interspecific synchrony was identified for negatively correlated species pairs. Remarkably, some species pairs were observed to display high intraspecific

synchrony between site pairs, while having strong negative interspecific correlations (the datapoints in the bottom right of figure 3.13: Right). There are mechanisms which may explain this. These mechanisms can be understood by considering a perfect negative correlation (r = -1). To achieve perfect negative correlation, at two common sites, both species must be responding strongly to environmental cues, albeit in an inverse fashion. Therefore, greater negative synchrony relationships may be observed in species with high intraspecific synchrony owing to either (1) opposite reproductive responses to the same floral cue, (2) reproductive responses to different floral cues that negatively covary, or (3) reproductive responses to the same floral cue but with seedfall in different years. I consider reproductive responses to the same floral cue but with seedfall in different years to be the most likely cause of this pattern. Species whose seeds fall two years after floral initiation are likely to display negative correlation with species whose seeds fall one year after floral initiation if they share the same floral cue. Rimu is one species whose seeds are known to fall two years after floral initiation (Norton and Kelly 1988). Furthermore, Schauber et al. (2002) discovered that rimu was negatively correlated with many species whose seeds fall one year after floral initiation. This evidence supports my hypothesis that species pairs with high intraspecific synchrony, but high negative correlation between them, occur when species respond to the same floral cue, but seeds fall in different years.

The conservation of floral cues, and resulting synchrony, across species may be purely coincidental, however, some argue that this interspecific synchrony may in fact be adaptive. Species that gain selective reproductive advantages from synchronous seed production within species, may further increase this advantage by synchronising with closely related species (Shibata et al. 1998, Kelly et al. 2000). However, this concept has so far only been suggested to apply to closely related species that share a common seed predator. In that case, synchrony between species may increase the satiation of seed predators, increasing the reproductive

efficiency of the species in question. While there appears to be a consensus that this mechanism can improve reproductive efficiency, and should be selected for in species that share a common seed predator, Schauber et al. (2002) argues that there is no evidence to suggest that synchrony between many New Zealand species is indeed adaptive. Instead they argued that it might result from the paucity of potential environmental cues which are available for plants to use that give good intra-specific synchrony over ecologically relevant spatial scales.

While the positive relationship between intraspecific and interspecific synchrony observed in the current study is likely due to conservation of floral cues among the synchronous study species, I do not suggest this is an adaptive characteristic. The study species have few common generalist seed predators (Beveridge 1964, Webb and Kelly 1993), therefore, adaptive synchrony within species has more likely evolved independently through advantages of economies of scale relating factors such as wind pollination efficiency and animal dispersal (Kelly 1994, Kelly et al. 2001). While ship rats (*Rattus rattus*) are known to destroy the seeds of many species in broadleaf-podocarp forests (including rimu, matai, miro, and kahikatea) (Beveridge 1964, Sweetapple and Nugent 2007), their recent introduction in the late 19th century (Atkinson 1973) leaves inadequate time for any significant evolutionary response by New Zealand's tree species. Therefore, it seems most likely that species synchronise intraspecifically due to selective reproductive advantages, and interspecifically due to a paucity of floral cues. As a result, there is a positive relationship between intraspecific and interspecific synchrony.

4 Floral cues

4.1 Introduction

Masting species achieve synchrony between individuals by synchronising reproductive efforts with external floral cues (Schauber et al. 2002). Weather conditions, in particular those relating to temperature, are suggested to be the most likely cue, as they are autocorrelated over large spatial scales and are influential to metabolic processes such as photosynthesis and growth in plants (Schauber et al. 2002). As I have previously shown, some species in broadleaf-podocarp forests display high levels of synchrony between populations (Chapter 3: Figure 3.3). This is likely achieved by synchronising their reproductive effort with such external floral cues.

Floral cues are often related in some way to the temperature during floral induction, this being the summer prior to seed production. The relationship between seed production and variation in summer temperatures has been shown in species of *Chionochloa* (Schauber et al. 2002, Kelly et al. 2008b), rimu (Norton and Kelly 1988), *Fagus* (Masaki et al. 2008), *Nothofagus*, *Celmisia*, *Phormium* and *Elaeocarpus* (Kelly et al. 2013).

Identification of floral cues has direct ecological management applications. Large seed events of masting species have been shown to significantly increase predator abundances, and subsequently predation rates on native New Zealand birds (O'Donnell and Phillipson 1996, Wilson et al. 1998). By understanding the floral cues responsible for these large seed events, we may predict their occurrence, allowing for pest management actions to be taken prior to bird loss.

However, with the exception of rimu (Norton and Kelly 1988), there have been no attempts made to identify the floral cue for the species of broadleaf-podocarp forests. To rectify this, I will test previously developed weather models, based on summer temperatures, on the seedfall patterns of my study species.

4.2 Methods

Datasets were all checked with the methodology described in Chapter 2: 2.2.1. Only species with at least 20 years of data (across all sites/datasets) were included in this study (Table 2.1). All data was log(+1) transformed prior to analysis.

GLMMs were run using weather data from the nearest virtual climate station (weather data collection described in Chapter1: 1.4.3 Weather data). All models used monitoring site as a random term, as the focus was on within site variation, not between. Including the random term allows for the structure of the data, where sites serve as replicates for species.

Four previously developed models involving mean summer air temperature were selected for testing including T1, T2, 2T, and ΔT. The T1 model used a single variable, mean air temperature of the summer one year prior (T_{n-1}). The T2 model also used a single variable, mean air temperature of the summer two years prior (T_{n-2}). The 2T model included two variables, the mean air temperature of the summer (T_{n-1}) one year prior, and the mean air temperature of the summer the two years prior (T_{n-2}). The ΔT model used a single variable, the mean air temperature of the summer one year prior minus the mean air temperature of the summer two years prior ($T_{n-1} - T_{n-2}$). Mean summer air temperature was calculated as the mean of the minimum and maximum daily air temperatures for the months of the austral summer, December-March (inclusive). These months were chosen to match those used in Kelly et al. (2013).

Models were tested for significance, then compared by marginal R^2 values and AIC scores.

4.3 Results

The results of the GLMM identified that seedfall of only a single species, kahikatea, was significantly related to any of the summer temperature models tested (Table 4.1). Both the

summer air temperature one year before (T_{n-1}) and the summer air temperature two years before (T_{n-2}), were significantly related to kahikatea seedfall when included in the same model (2T). However, neither of these variables were significant independently (T1 and T2 models). Seedfall of kahikatea was also significantly related to the difference in summer air temperatures between the previous year and two years previously (ΔT). The best model for kahikatea seedfall (AIC and R^2_m) was ΔT (Table 4.1). The ΔT model had a positive relationship with kahikatea seedfall at all sites (Table 4.1).

Table 4.1 The results of GLMM for the five models included in the study. R^2_m, is the marginal R^2 (variance explained by the fixed terms in the model). All models use monitoring site as a random term. Note that the 2T model has a p value for each variable of its two variables: T_{n-1} and T_{n-2}.

Species	R^2_m T1	R^2_m T2	R^2_m 2T	R^2_m Δt	p T1	p T2	p 2T(T_{n-1})	p 2T(T_{n-2})	p Δ t	Best AIC
Hinau	0.02	0.05	0.04	0.01	0.60	0.35	0.96	0.44	0.68	T2
Kahikatea	0.07	0.05	0.15	0.16	0.21	0.26	**0.01**	**0.02**	**<0.01**	ΔT
Matai	<0.01	0.07	0.10	0.08	0.89	0.21	0.33	0.12	0.18	ΔT
Miro	<0.01	0.07	0.10	0.08	0.74	0.32	0.74	0.33	0.65	T1
Rimu	0.01	0.04	0.02	0.02	0.74	0.41	0.55	0.40	0.41	ΔT
Supplejack	0.19	0.10	0.23	0.00	0.07	0.17	0.17	0.55	0.65	T1
Tawa	<0.01	<0.01	<0.01	<0.01	0.96	0.88	>0.99	0.89	0.93	T2

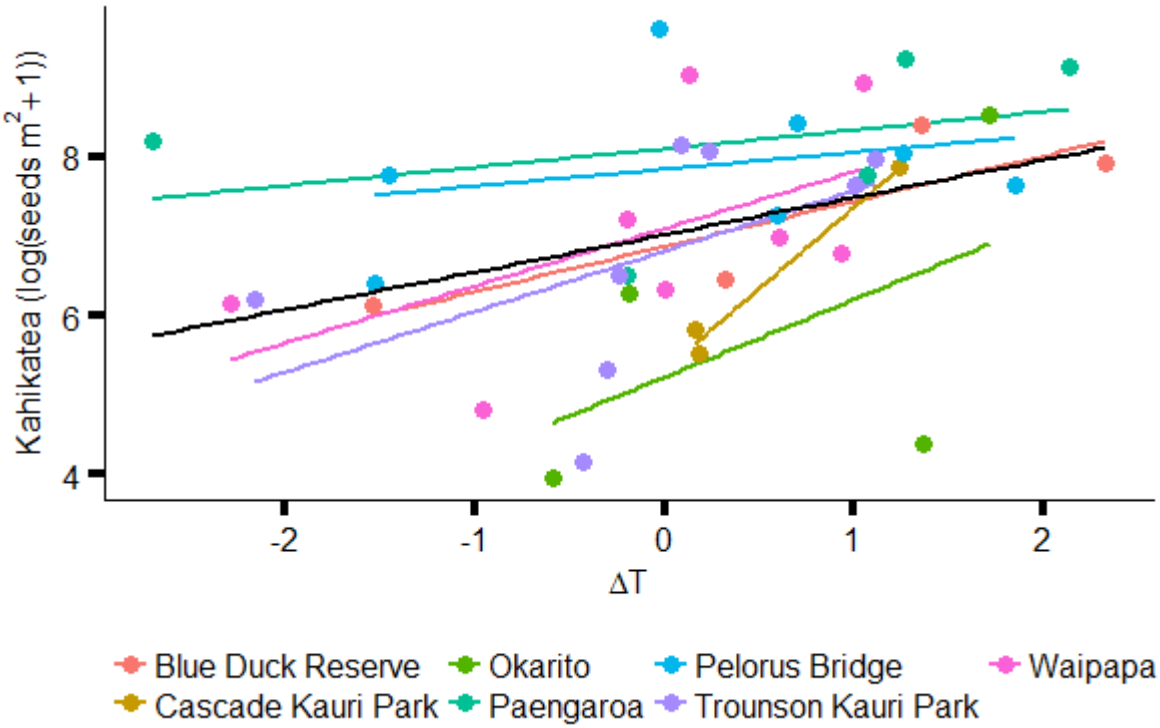

Figure 4.1 The relationship of the difference between the two previous years mean summer air temperatures (ΔT) and seedfall of kahikatea. The black line is a linear model showing the mean of the relationship among all sites.

4.4 Conclusion

Mean summer air temperature had a significant relationship with seedfall in kahikatea. Warm summers, preceded by cool summers (ΔT), was identified as the best model for this relationship. This is the first time kahikatea seedfall has been shown to be significantly related to summer temperatures. This finding can also explain the high level of synchrony I observed between distant kahikatea populations (Chapter 3, Figure 3.3). However, I also observed high intraspecific synchrony in rimu, hinau, and supplejack (Chapter 3, Figure 3.3), indicating the presence of floral cues for these species.

Norton and Kelly (1988) identified that years of large seedfall in rimu are related to low seed production and cool temperatures two years (T_{n-1}) prior to seedfall and warm summers in the year of seedfall (T_n). Norton (1985) attributed the relationship between seed production and

the previous years seedfall to long seed development times, leading to competition between overlapping cohorts. While I tested a relationship between the difference in air temperatures of the summer the year before seedfall and of the year prior to that (ΔT), it was not significant for rimu. However, following Kelly et al (2013) I did not test for effects of the temperatures during the year of seedfall, which would not pick up possible effects of the seedfall season like that above for rimu. This indicates that the interaction of seed production between years discovered by Norton and Kelly (1988), plays a strong role in determining rimu seed output. Seed development times for hinau and supplejack are not known, however, interactions between previous years of seed production is one hypothesis that may explain their lack of relationship with any of the models tested. While cues relating to other weather variables are possible (Kelly et al. 2013), this is a more unlikely hypothesis. For most species that display masting behaviour, the floral cue for large seed years is related to summer temperatures (Norton and Kelly 1988, Schauber et al. 2002, Selås et al. 2002, Masaki et al. 2008, Kelly et al. 2013).

5 Conclusion:

My thesis has advanced knowledge of masting characteristics in the little studied species that make up New Zealand's broadleaf-podocarp forests. By quantifying the variability of these species, as well as how that varies spatially within species, and between species, I have fulfilled some of the original aims of the thesis. The results of my study have ecological significance and may be used to inform future seed monitoring and masting research.

5.1 Ecological significance

Species in New Zealand's broadleaf-podocarp forests differ greatly in their among-year variability of seed production. My study has identified species that are more variable than expected in the absence of natural selection (*Hoheria* sp, kohekohe, hinau, tawari, tanekaha, and mountain beech), and others that are less variable than expected if there is no selection (mahoe, totara, karaka, *Pittosporum* sp, miro, and needle-leaved totara) (Kelly et al. 2001). The variability of seed production for these species is likely to have significant effects on their local ecosystems.

Highly variable seed production has been shown to influence predator abundances in New Zealand forests through bottom-up ecosystem effects (King 1983, Dilks et al. 2003, Harper 2005). Years of high seed production, leading to increased predator abundance has also been suggested to alter predation rates on native bird species. Wilson et al. (1998) showed that high seed years in mountain beech were associated with increased predations rates on a native bird species, kaka. Furthermore, Wilson et al. (1998) hypothesised that predation pressure in non-beech forests would be greater, owing to a more constant supply of resources provided by tree species, maintaining predator populations through bottom-up effects. My thesis may provide more information on how this mechanism may operate in broadleaf-podocarp forests.

I identified many species in broadleaf-podocarp forests with high CV values comparable to the CV value of mountain beech, which may suggest that resources are also highly variable in these forests. However, the extreme resource pulses observed in beech forests are partially due beech species dominating the forest canopy (Wilson et al. 1998). The combination between lack of alternative resources, and the high synchrony of seed production between beech species (Schauber et al. 2002), results in variable resources, highly related to the CV of beech species. Broadleaf-podocarp forests are, by comparison, much more diverse in the number of species present. Therefore, when trying to understand the resource dynamics in these forest, consideration must be given to the variability of species, but also to the synchrony between species.

My thesis has identified strong correlations between the yearly seed production in many broadleaf-podocarp species. However, if the ecological interest is in the size of the resource pulses in these forests, it is the synchrony between highly variable species that is most important. My finding that CV has no relationship with interspecific synchrony tells us that highly variable species in these forests do not consistently synchronise their seed production efforts. Therefore, despite variable seed production comparable to beech trees occurring within the broadleaf-podocarp forests species, I do not expect that the community-wide level variability of resources will be as great as in beech forests.

This understanding has implications on how predator species are managed in these forests. In beech forests, pest management efficiency may be increased by predicting mast years in beech trees, and adjusting management effort accordingly (Elliott et al. 2001). However, I have shown resource levels are likely more consistent in broadleaf-podocarp forests by comparison. I suggest that management efforts, therefore, need not be as variable in these forests.

Variable seed production from species in broadleaf-podocarp forests is likely to have direct effects on frugivorous bird species. Most New Zealand forest birds have diets which consist, at least partially, of fruits from native tree species (Clout and Hay 1989, O'Donnell and Phillipson 1996). Therefore, variability of seed production of broadleaf-podocarp forest species creates variable resources for these birds. The effect of variable seed production on bird populations is dependent the diet of the species.

5.2 Recommendations for future seed monitoring and mast research

My thesis has highlighted the importance of tailoring seed monitoring to match the purpose, be it ecological management, or advancing knowledge in the field of masting.

I found that synchrony of seed production between populations is high in hinau, kahikatea, rimu, and supplejack. These species displayed synchrony between populations, even when monitoring sites were >500 km apart. Furthermore, no relationship was found between intraspecific synchrony and distance, for any of my study species. If the purpose of seed monitoring is simply to determine if a high seed year has occurred in these species, perhaps for ecological management programs, I suggest that seed monitoring for these species does not need to be spatially intensive.

However, if the purpose of seed monitoring is to acquire data for research purposes, the research questions should determine the sampling design. In my study I identified no relationship between site productivity and variability of seed production, despite this relationship being previously reported in the literature (Allen and Platt 1990, Webb and Kelly 1993, Mencuccini et al. 1995, Sullivan and Kelly 2000). I attributed this to my inability to test for the relationship within individual species, due to low number of replicates per species. For future studies on masting that have a spatial component, I therefore recommend seed monitoring be spatially intensive, from numerous sites.

My study of interspecific synchrony identified that species' relationships can be inconsistent among sites. Therefore, if future research entails species comparisons, I recommend that sampling occurs at many sites, ideally over a large spatial range. Future studies of synchrony, be it inter or intra, must also be wary of the number of years of seed data available. While my study of interspecific synchrony identified strong correlations between species, Bonferroni correction rendered these relationships insignificant. As the number of significant results prior to Bonferroni correction was significantly greater than expected, it is likely that the test suffered from a lack of sampling years. However, as the datasets used in the current study are ongoing, they will be a valuable resource for testing interspecific synchrony in the future.

The final aspect of seed monitoring I wish to emphasise is the importance of sampling intensity within populations. As masting involves the synchrony of seed production between individuals within a population (Kelly and Sork 2002, Koenig et al. 2003, Koenig et al. 2015), it is important to sample by collecting seeds from multiple individual trees. To be sure of the number of individuals contributing to each seed sample, collection devices should be installed under individual trees, and constant in their positioning through years.

To conclude, there should be three primary considerations when initiating future seed monitoring, with the relative importance of each is depending on the purpose of collection. These are:

1. Number of seed monitoring sites
2. Number of years of seed monitoring
3. Number of individuals sampled

However, to some extent these points highlight how difficult it is to study mast seeding, as it is a multi-year phenomenon and long runs of data (ideally >10 years) are required even to

describe a single species at a single site. In order to look at spatial correlation within a species, and synchrony among different species, multiple species must be measured consistently for many years at multiple sites. The lack of such data collection before about 2005 has meant that little was known about masting by species in New Zealand's podocarp-broadleaf forests. The network of seed collection stations set up after 2006 by the Department of Conservation, and analysed for the first time in this thesis, is beginning to provide answers. The longer those stations are monitored, the clearer the answers will be.

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Appendices

Appendix A

Complete list of all intraspecific synchrony values (Pearson r) for species with multiple datasets, including the distance between monitoring sites. Species and sites filtered as per the conditions described in 3.2.1.1: Quantifying intraspecific synchrony. Years represents the number of overlapping years for each site combination, and hence sample size (n) for the correlation.

Species	Site one	Site two	Pearson r	Distance (km)	Years (n)
Hinau	Blue Duck Reserve	Otamatuna	0.83	519.54	5
Hinau	Blue Duck Reserve	Pelorus Bridge	0.96	105.62	5
Hinau	Otamatuna	Pelorus Bridge	0.64	449.58	7
Hinau	Blue Duck Reserve	Waipapa	0.79	447.13	5
Hinau	Otamatuna	Waipapa	0.24	135.48	8
Hinau	Pelorus Bridge	Waipapa	0.65	359.96	7
Kahikatea	Blue Duck Reserve	Paengaroa	0.98	330.65	4
Kahikatea	Blue Duck Reserve	Pelorus Bridge	0.88	105.62	5
Kahikatea	Okarito	Pelorus Bridge	0.63	350.97	4
Kahikatea	Paengaroa	Pelorus Bridge	0.64	258.30	5
Kahikatea	Blue Duck Reserve	Trounson Kauri Park	0.93	722.77	5
Kahikatea	Okarito	Trounson Kauri Park	0.90	886.02	4
Kahikatea	Paengaroa	Trounson Kauri Park	0.98	472.04	5
Kahikatea	Pelorus Bridge	Trounson Kauri Park	0.73	618.50	7
Kahikatea	Blue Duck Reserve	Waipapa	0.80	447.13	5
Kahikatea	Okarito	Waipapa	0.17	699.01	4
Kahikatea	Paengaroa	Waipapa	0.38	132.17	5
Kahikatea	Pelorus Bridge	Waipapa	0.83	359.96	7
Kahikatea	Trounson Kauri Park	Waipapa	0.50	349.97	8
Matai	Blue Duck Reserve	Paengaroa	<-0.99	330.65	4
Matai	Blue Duck Reserve	Pelorus Bridge	-0.79	105.62	5
Matai	Paengaroa	Pelorus Bridge	0.82	258.30	5
Matai	Blue Duck Reserve	Waipapa	0.29	447.13	5
Matai	Paengaroa	Waipapa	-0.19	132.17	5
Matai	Pelorus Bridge	Waipapa	0.44	359.96	7
Miro	Okarito	Otamatuna	-0.67	799.28	4
Miro	Okarito	Pelorus Bridge	-0.81	350.97	4
Miro	Otamatuna	Pelorus Bridge	0.47	449.58	7
Miro	Okarito	Waipapa	-0.47	699.01	4
Miro	Otamatuna	Waipapa	0.02	135.48	8
Miro	Pelorus Bridge	Waipapa	-0.12	359.96	7
Rimu	Blue Duck Reserve	Otamatuna	0.72	519.54	5
Rimu	Blue Duck Reserve	Pelorus Bridge	0.98	105.62	5
Rimu	Otamatuna	Pelorus Bridge	0.66	449.58	7

Rimu	Blue Duck Reserve	Waipapa	0.70	447.13	5
Rimu	Otamatuna	Waipapa	0.82	135.48	8
Rimu	Pelorus Bridge	Waipapa	0.76	359.96	7
Supplejack	Blue Duck Reserve	Otamatuna	0.47	519.54	5
Supplejack	Blue Duck Reserve	Waipapa	0.84	447.13	5
Supplejack	Otamatuna	Waipapa	0.51	135.48	8
Tawa	Blue Duck Reserve	Otamatuna	-0.31	519.54	5
Tawa	Blue Duck Reserve	Pelorus Bridge	-0.69	105.62	5
Tawa	Otamatuna	Pelorus Bridge	0.29	449.58	7
Tawa	Blue Duck Reserve	Trounson Kauri Park	-0.06	722.77	5
Tawa	Otamatuna	Trounson Kauri Park	-0.37	425.41	8
Tawa	Pelorus Bridge	Trounson Kauri Park	-0.10	618.50	7
Tawa	Blue Duck Reserve	Waipapa	-0.09	447.13	5
Tawa	Otamatuna	Waipapa	0.52	135.48	8
Tawa	Pelorus Bridge	Waipapa	0.12	359.96	7
Tawa	Trounson Kauri Park	Waipapa	-0.67	349.97	8
Totara	Blue Duck Reserve	Waipapa	0.78	447.13	5

Appendix B

Complete list of all 141 calculated interspecific synchrony values (Pearson r). Species and sites filtered to the conditions described in 3.2.2.1: Quantifying interspecific synchrony. Table sorted alphabetically by "Species one".

Species one	Species two	Monitoring site	Pearson r	Years (n)
Black Maire	Coprosma grandifolia	Paengaroa	0.47	5
Black Maire	Hoheria sp	Paengaroa	0.13	5
Black Maire	Kahikatea	Paengaroa	0.39	5
Black Maire	Lowland ribbonwood	Paengaroa	0.22	5
Black Maire	Matai	Paengaroa	0.45	5
Black Maire	Pittosporum sp	Paengaroa	-0.55	5
Coprosma grandifolia	Hoheria sp	Paengaroa	0.50	5
Coprosma grandifolia	Kahikatea	Paengaroa	-0.29	5
Coprosma grandifolia	Lowland ribbonwood	Paengaroa	-0.48	5
Coprosma grandifolia	Matai	Paengaroa	0.59	5
Coprosma grandifolia	Pittosporum sp	Paengaroa	-0.55	5
Hinau	Kahikatea	Blue Duck Reserve	0.84	4
Hinau	Mahoe	Blue Duck Reserve	-0.98	4
Hinau	Matai	Blue Duck Reserve	0.97	4
Hinau	Mountain Beech	Blue Duck Reserve	0.81	4
Hinau	Rimu	Blue Duck Reserve	0.78	4
Hinau	Supplejack	Blue Duck Reserve	0.68	4

Hinau	Tawa	Blue Duck Reserve	-0.93	4
Hinau	Totara	Blue Duck Reserve	0.87	4
Hinau	Miro	Otamatuna	-0.25	8
Hinau	Mountain Totara	Otamatuna	-0.37	8
Hinau	Red Beech	Otamatuna	0.73	8
Hinau	Rimu	Otamatuna	0.37	8
Hinau	Supplejack	Otamatuna	0.51	8
Hinau	Tawa	Otamatuna	0.36	8
Hinau	Tawari	Otamatuna	0.41	8
Hinau	Kahikatea	Pelorus Bridge	0.66	7
Hinau	Matai	Pelorus Bridge	-0.76	7
Hinau	Miro	Pelorus Bridge	0.34	7
Hinau	Rimu	Pelorus Bridge	0.78	7
Hinau	Tawa	Pelorus Bridge	-0.11	7
Hinau	Kahikatea	Waipapa	0.34	8
Hinau	Matai	Waipapa	0.00	8
Hinau	Miro	Waipapa	0.02	8
Hinau	Rimu	Waipapa	0.36	8
Hinau	Supplejack	Waipapa	0.27	8
Hinau	Tawa	Waipapa	0.13	8
Hinau	Totara	Waipapa	0.67	8
Hoheria sp	Kahikatea	Paengaroa	-0.55	5
Hoheria sp	Lowland ribbonwood	Paengaroa	-0.56	5
Hoheria sp	Matai	Paengaroa	0.22	5
Hoheria sp	Pittosporum sp	Paengaroa	0.41	5
Kahikatea	Mahoe	Blue Duck Reserve	-0.92	4
Kahikatea	Matai	Blue Duck Reserve	0.92	4
Kahikatea	Mountain Beech	Blue Duck Reserve	1.00	4
Kahikatea	Rimu	Blue Duck Reserve	0.35	4
Kahikatea	Supplejack	Blue Duck Reserve	0.20	4
Kahikatea	Tawa	Blue Duck Reserve	-0.90	4
Kahikatea	Totara	Blue Duck Reserve	0.66	4
Kahikatea	Miro	Okarito	0.18	4
Kahikatea	Needle-leaved totara	Okarito	0.80	4
Kahikatea	Lowland ribbonwood	Paengaroa	0.98	5
Kahikatea	Matai	Paengaroa	-0.53	5
Kahikatea	Pittosporum sp	Paengaroa	-0.22	5
Kahikatea	Matai	Pelorus Bridge	-0.34	7
Kahikatea	Miro	Pelorus Bridge	0.45	7
Kahikatea	Rimu	Pelorus Bridge	0.67	7
Kahikatea	Tawa	Pelorus Bridge	0.54	7
Kahikatea	Kauri	Trounson Kauri Park	-0.31	8
Kahikatea	Kohekohe	Trounson Kauri Park	0.15	8
Kahikatea	Taraire	Trounson Kauri Park	-0.16	8
Kahikatea	Tawa	Trounson Kauri Park	0.07	8
Kahikatea	Matai	Waipapa	-0.30	8

Kahikatea	Miro	Waipapa	0.82	8
Kahikatea	Rimu	Waipapa	0.65	8
Kahikatea	Supplejack	Waipapa	0.48	8
Kahikatea	Tawa	Waipapa	0.44	8
Kahikatea	Totara	Waipapa	0.67	8
Kauri	Kohekohe	Trounson Kauri Park	-0.07	8
Kauri	Taraire	Trounson Kauri Park	0.32	8
Kauri	Tawa	Trounson Kauri Park	-0.53	8
Kohekohe	Taraire	Trounson Kauri Park	0.47	8
Kohekohe	Tawa	Trounson Kauri Park	-0.35	8
Lowland ribbonwood	Matai	Paengaroa	-0.67	5
Lowland ribbonwood	Pittosporum sp	Paengaroa	-0.02	5
Mahoe	Matai	Blue Duck Reserve	-0.97	4
Mahoe	Mountain Beech	Blue Duck Reserve	-0.89	4
Mahoe	Rimu	Blue Duck Reserve	-0.69	4
Mahoe	Supplejack	Blue Duck Reserve	-0.58	4
Mahoe	Tawa	Blue Duck Reserve	0.97	4
Mahoe	Totara	Blue Duck Reserve	-0.87	4
Matai	Mountain Beech	Blue Duck Reserve	0.90	4
Matai	Rimu	Blue Duck Reserve	0.60	4
Matai	Supplejack	Blue Duck Reserve	0.49	4
Matai	Tawa	Blue Duck Reserve	-0.90	4
Matai	Totara	Blue Duck Reserve	0.74	4
Matai	Pittosporum sp	Paengaroa	-0.56	5
Matai	Miro	Pelorus Bridge	-0.17	7
Matai	Rimu	Pelorus Bridge	-0.45	7
Matai	Tawa	Pelorus Bridge	0.51	7
Matai	Miro	Waipapa	0.00	8
Matai	Rimu	Waipapa	-0.50	8
Matai	Supplejack	Waipapa	-0.23	8
Matai	Tawa	Waipapa	0.09	8
Matai	Totara	Waipapa	-0.31	8
Miro	Needle-leaved totara	Okarito	0.00	4
Miro	Mountain Totara	Otamatuna	0.33	8
Miro	Red Beech	Otamatuna	0.06	8
Miro	Rimu	Otamatuna	0.72	8
Miro	Supplejack	Otamatuna	0.46	8
Miro	Tawa	Otamatuna	0.52	8
Miro	Tawari	Otamatuna	0.46	8
Miro	Rimu	Pelorus Bridge	0.81	7
Miro	Tawa	Pelorus Bridge	0.03	7
Miro	Rimu	Waipapa	0.50	8
Miro	Supplejack	Waipapa	0.06	8
Miro	Tawa	Waipapa	0.33	8
Miro	Totara	Waipapa	0.55	8
Mountain Beech	Rimu	Blue Duck Reserve	0.29	4

Mountain Beech	Supplejack	Blue Duck Reserve	0.15	4
Mountain Beech	Tawa	Blue Duck Reserve	-0.88	4
Mountain Beech	Totara	Blue Duck Reserve	0.61	4
Mountain Totara	Red Beech	Otamatuna	0.24	8
Mountain Totara	Rimu	Otamatuna	0.14	8
Mountain Totara	Supplejack	Otamatuna	0.25	8
Mountain Totara	Tawa	Otamatuna	0.18	8
Mountain Totara	Tawari	Otamatuna	0.46	8
Red Beech	Rimu	Otamatuna	0.55	8
Red Beech	Supplejack	Otamatuna	0.79	8
Red Beech	Tawa	Otamatuna	0.75	8
Red Beech	Tawari	Otamatuna	0.70	8
Rimu	Supplejack	Blue Duck Reserve	0.99	4
Rimu	Tawa	Blue Duck Reserve	-0.67	4
Rimu	Totara	Blue Duck Reserve	0.88	4
Rimu	Supplejack	Otamatuna	0.57	8
Rimu	Tawa	Otamatuna	0.71	8
Rimu	Tawari	Otamatuna	0.82	8
Rimu	Tawa	Pelorus Bridge	-0.03	7
Rimu	Supplejack	Waipapa	0.29	8
Rimu	Tawa	Waipapa	-0.06	8
Rimu	Totara	Waipapa	0.61	8
Supplejack	Tawa	Blue Duck Reserve	-0.55	4
Supplejack	Totara	Blue Duck Reserve	0.81	4
Supplejack	Tawa	Otamatuna	0.83	8
Supplejack	Tawari	Otamatuna	0.59	8
Supplejack	Tawa	Waipapa	0.65	8
Supplejack	Totara	Waipapa	0.27	8
Taraire	Tawa	Trounson Kauri Park	0.03	8
Tawa	Totara	Blue Duck Reserve	-0.91	4
Tawa	Tawari	Otamatuna	0.64	8
Tawa	Totara	Waipapa	0.38	8